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SOMETHING FOR HOPE

At the present rate it must come to pass,
And that right soon, that the meadowsweet
And steeple bush, not good to eat,
Will have crowded out the edible grass.

Then all there is to do is wait
For maple, birch, and spruce to push
Through meadowsweet and steeple bush
And crowd them out at a similar rate.

No plow among these rocks would pay.
So busy yourself with other things
While the trees put on their wooden rings
And with long-sleeved branches hold their sway.

Then cut down the trees when lumber grown,
And there's your pristine earth all freed
From lovely blooming but wasteful weed
And ready again for the grass to own.

A cycle we'll say of a hundred years.
Thus, foresight does it and laissez-faire,
A virtue in which we all may share
Unless a government interferes.

Patience and looking away ahead,
And leaving some things to take their course.
Hope may not nourish a cow or horse,
But *spes alit agricolam* 'tis said.

-Robert Frost

"... I survived until I took the degree of Doctor of Philosophy in 1903. The meaning of this degree is that the recipient of instruction is examined for the last time in his life, and is pronounced completely full. After this, no new ideas can be imparted to him."

Stephen Leacock, 1912
Preface to *Sunshine Sketches of a Little Town*

University of Alberta

PATTERNS OF BOREAL FOREST TREE SPECIES IN SPACE AND TIME

by

Lorne Richard Little ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Doctor of Philosophy

in

Environmental Biology and Ecology

Department of Biological Sciences

Spring 2000

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Patterns of Boreal Forest Trees in Space and Time* submitted by Lorne Richard Little in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Environmental Biology and Ecology.

This is dedicated to my family: parents and brothers,
but especially to Emma

Abstract

Analysis, and ecological implications of spatio-temporal pattern in plant establishment were examined. Only trees were considered because time of establishment could be estimated from the count of annual rings. Data sets came from post-fire boreal forest, and consisted of stem positions, and time of establishment in a grid of quadrats.

The initial approach to analysis used join count statistics, where each pair of plants was characterized by a two-factor join, describing association in space and time. For a random spatio-temporal distribution, the mean and variance for two-factor joins were derived based on earlier work for one-factor joins. Observed spatio-temporal distributions from several data sets were then examined. A second analysis approach consisted of comparing the spatial pattern of different stem ages to that of the initial conspecific establishers. The results of this analysis showed how establishment changed in time. I expected different patterns to be associated according to certain species' characteristics. Finally, I examined the degree that competition operates among initially establishing stems.

Two-factor join count statistics were used to obtain the rate of expansion of a *Populus balsamifera* clone into an adjacent grassland. However, in more complicated circumstances, as in a post-fire boreal forest, results from join count statistics were difficult to interpret. Using the second approach, clonal *Populus* ramets appeared to establish away from the initial establishers in surges, contrary to what was found at a grassland interface. Seed dispersed *Pinus banksiana* showed an initial, clustered surge in establishment. Although overall establishment decreased with time, the reduction was greatest near the initial establishers. Establishment of shade-tolerant *Picea* species showed little change in time. Intraspecific competition among the initial establishers was examined based on a

hypothesis of regular pattern among large, successful trees, but results unexpectedly showed spatially clustered pattern. Further analysis of large trees showed negative association between species, indicating either a response to habitat heterogeneity or interspecific competition.

Although ecological processes cannot be inferred from ecological pattern, the results of this thesis show that patterns, namely, spatial arrangments of different ages of trees, can be used to aid perception of ecological processes that are thought to occur.

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Many people, in countless manners, helped me to complete this thesis. In the academic aspect, foremost among these people is the person I saw the most of day in and day out Mark Dale. There were many other people who contributed to my academic environment, in such a large department and institution, but much came from Susan Hannon, Phil Lee, and Ross Wein. A very special thank-you is reserved for Christine Brodie, who let me use her MSc data. When it came to technicalities, as many are, I am indebted to Jeff Hoyem, Lorne LeClair, "Mac" McIntyre and Barry McCashin. P. Kitsco, D. Mucha, L. Goodchild and A. Dusek, all helped in data acquisition.

In personal affairs, my parents Mary Ann and Lorne Little have been there from the beginning, and my father was even there in my first field season. There were many graduate student colleagues, throughout the department that I enjoyed going through the grind with. Two office-mates deserve special mention, however, Brendan Wilson for his telemark skiing instructions, and Cheryl Smyth for her love of kimchi, and junk food. Finally, for her companionship in the past year, I am grateful to Emma, who has changed many things, making it an eventful year, indeed.

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TABLE OF CONTENTS

CHAPTER ONE

THESIS INTRODUCTION 1
References 12

CHAPTER TWO

BASIS FOR EXAMINING ASSOCIATION IN PLANT ESTABLISHMENT IN SPACE AND TIME: TWO-FACTOR JOIN COUNT STATISTICS

Introduction 15
Random Association of Black Cells on a Lattice 16
Conclusion 20
References 22

CHAPTER THREE

A METHOD FOR ANALYSING SPATIO-TEMPORAL PATTERN IN PLANT ESTABLISHMENT: AN EXAMPLE FROM A *POPULUS BALSAMIFERA* CLONE

Introduction 23
Methods 25
Results 32
Discussion 37
References 45

CHAPTER FOUR

ESTABLISHMENT AT DIFFERENT TIMES SINCE DISTURBANCE IN RELATION TO DISPERSAL AND SHADE TOLERANCE STRATEGIES OF BOREAL FOREST TREE SPECIES

Introduction 48
Methods 51
Results 59
Discussion 76
References 81

CHAPTER FIVE

UNEXPECTED SPATIAL PATTERN OF TREE SPECIES ARRANGEMENTS IN MULTI-SPECIES FORESTS

Introduction 85
Methods...87
Results 93
Discussion 108
References 112

CHAPTER SIX

THESIS SYNTHESIS..116
References 120

LIST OF TABLES

Table 1-1. Five classes of species mobility characterized by stem frequency in space and in time, as described by van der Maarel (1996). Frequency in time can also be viewed as inversely related to the variability of species presence in time..3

Table 2-1. The mean and variance for four selected two-factor (s,t) join classes on a 10 X 10 random lattice, p=0.2, and the statistics calculated from equations in text, and 1000 iterations of a randomization procedure..21

Table 4-1. Results of spatial pattern analysis of stems classified by age class, species and data set..60

Table 4-2. Association between species, dispersal and survival strategy, and the gap environment, measured as distance to nearest "large" tree...75

Table 5-1. Mean number of neighbouring stems, by stem class, that surround each stem of the focal stem class, in the Québec data set. Neighbour relationship was derived according to a Least Diagonal Neighbour Triangulation...103

Table 5-2. Mean distance from stems of the focal stem class to stem neighbouring stems, by stem class, in the Québec data set. Neighbour relationship was derived according to a Least Diagonal Neighbour Triangulation...104

Table 5-3. Mean number of neighbouring stems, by stem class, that surround each stem of the focal stem class, in the Alberta data set. Neighbour relationship was derived according to a Least Diagonal Neighbour Triangulation...105

Table 5-4. Mean distance from stems of the focal stem class to stem neighbouring stems, by stem class, in the Québec data set. Neighbour relationship was derived according to a Least Diagonal Neighbour Triangulation...106

LIST OF FIGURES

Figure 1-1. Pattern at multiple scales in which the points are clustered at the smallest small scale. At a slightly larger scale, the clusters are regularly arranged, and at a still larger scale they are clumped toward the top of the figure 7

Figure 1-2. A grid containing nominal, binary, data where each cell has value "X" or is blank. All joins, of length one cell, that connect cells with X's are also shown (based on Sokal and Oden, 1978)....9

Figure 2-1. A subdivided 15 X 15 lattice. The number of companion joins with which $g_{i,j}$ joins of class s=3, t=3 share a single cell is indicated by the number in the respective subdivision. For example, join A or $g_{3,3}$ may share a single cell with three other joins. Join B, $g_{12,3}$, can share a single cell with two other joins, and join C, $g_{4,12}$, with four other joins. 19

Figure 3-1. Artificial spatio-temporal pattern of **a**. lattice C and **b**. lattice D. Black cells represent establishment....29

Figure 3-2. Lattice representation of spatio-temporal arrangements of *P. balsamifera* along three transects, at Ministik Bird Sanctuary, Alberta, Canada. Black cells represent establishment. Quadrats represent 0.5 m spatial intervals 31

Figure 3-3. Two-factor correlograms for the analysis of **a**. lattice B (no noise) and **b**. lattice C (with noise), using the fully randomized cell model for each join class, black circles represent positive autocorrelation, and white circles negative....33

Figure 3-4. Two-factor correlograms for the analysis of artificial data lattice D using **a**. the fully randomized cell model, **b**. the uniform row model and **c**. the top-black model. For each join class, black circles represent positive autocorrelation, and white circles negative 35

Figure 3-5. Two-factor correlograms of *P. balsamifera* spatio-temporal arrangement in the three transects, using the three random models. Black circles represent positive autocorrelation, and white circles negative....36

Figure 3-6. Hypothetical spatio-temporal arrangement of a transect in which 3 quadrats are initially colonized, and nucleate in both directions of the transect to eventually coalesce.... 38

Figure 3-7. Two-factor correlograms using the Full Randomized Cell model for join count statistics on data from a. transect 1, and b. transect 2 of a post-fire boreal forest site at Wandering River, Alberta....43

Figure 3-8. Two-factor correlograms using the Uniform Row model for join count statistics on data from a. transect 1, and b. transect 2 of a post-fire boreal forest site at Wandering River, Alberta..44

Figure 4-1. Two orientations of the Haar wavelet 53

Figure 4-2. Illustration of the fourth-corner problem (Legendre et al.1997) 58

Figure 4-3. Age class frequency distribution of the three tree species at the Alberta site 61

Figure 4-4. Wavlet scalogram of **a**. artificial transect 1, **b**. mean of the three artificial transects, and **c**. actual values along the artificial transects 63

Figure 4-5. Mean wavelet scalogram across contiguous transects in the Alberta site for *P. tremuloides* and *P. mariana* 64

Figure 4-6. Spatial distribution and bivariate analysis between the oldest age class of stems and each of the younger age classes for *P. mariana* of Légèr and Payette (1981) 65

Figure 4-7. Spatial distribution and bivariate analysis between the oldest age class of stems and each of the **a**. five youngest, and **b**. five oldest age classes of *P. balsamifera* stems in the Québec data set 67, 67b

Figure 4-8. Spatial distribution and bivariate analysis between the oldest age class of stems and each younger age class of **a**. *P. mariana* stems, and **b**. *P. glauca* stems, in the Québec data set 68, 68b

Figure 4-9. Spatial distribution and bivariate spatial association between the oldest age class of stems and each younger age classes of *P. banksiana* in the Alberta site.......................69

Figure 4-10. Spatial distribution and bivariate spatial association between the oldest age class of stems and each younger age classes of *P. tremuloides* in the Alberta site 70

Figure 4-11. Spatial distribution and bivariate spatial association between the oldest age class of stems and each younger age classes of *P. mariana* in the Alberta site.................72

Figure 4-12. The gap environment at the Alberta site where quadrats were assigned distance to the nearest "large" tree (i.e. >5 cm dgh) 73

Figure 4-13. Frequency distributions of quadrats according to distance to nearest "large" tree (i.e. >5 cm dgh)..74

Figure 5-1. Stem positions of large and small *P. banksiana* and *P. tremuloides* in the Alberta site that were used to define neighbourhood relationships by Least Diagonal Neightbour Triangulation..91

Figure 5-2. Stem positions of large and small *P. balsamifera*, *P. mariana* and *P. glauca* in the Quebec site that were used to define neighbourhood relationships by Least Diagonal Neightbour Triangulation..92

Figure 5-3. Frequency distributions of canopy tree species in 3 year old age classes, and 2 size classes, at the Québec and Alberta sites 94

Figure 5-4. Spatial arrangements of the canopy species stems with the potential to obtain large status. Stem size class is indicated...95

Figure 5-5. Univariate spatial pattern analysis, under a hypothesis of complete spatial randomness, for large individuals of the canopy species at both sites..............................96

Figure 5-6. Bivariate spatial association, under a hypothesis of complete spatial randomness, between large stems of both species at the Alberta site, and between all stems of both species..98

Figure 5-7. Bivariate spatial association, under a hypothesis of complete spatial randomness, between large stems of each species pair, and all stems of each species pair at the Québec site...99

Figure 5-8. Univariate spatial analyses, at both sites, under a null hypothesis of random success..101

Figure 5-9. Bivariate spatial analyses between the large stems of different species combinations, in both sites, under a null hypothesis of random success........................102

CHAPTER ONE

Thesis Introduction

Individual plants are capable of many kinds of movement. Phototropism and geotropism are two of the most well-known ways, but there is also the less common thigmotropism, displayed by vines as they wind up trees, nyctasy displayed as plants move to different postures at night, and the dramatic quick movement as a Venus Flytrap or *Mimosa pudica* responds to touch (Darwin 1881, Salisbury and Ross 1992). Another striking phenomena of plant biology, perhaps due to the small spatial and time scale of human experience, is that populations of plants also move. As with individual plants, populations move in many ways. For example, at large spatial scales, long-term shifts in species' distributions, especially following the retreat of the continental ice sheets, are evident from pollen data (Bennett 1998). Simple propagule diffusion is unable to account for the estimated high rates of movement (Skellam 1951, Bennett 1986, Cain et al. 1998), and other mechanisms, e.g. animal transport, are thought to play an important role. The result is that this movement is highly contingent and unpredictable, depending on improbable and infrequent events (Cain et al. 1998).

Plant population movement also occurs at much smaller spatial scales, and often in a more predictable manner. For example, a population may expand into new unvegetated areas, as species colonize in sand dunes or the area left in the wake of a retreating glacier. After a period of time, other species may enter the area as the colonizers change the

environmental conditions in such a way to favour establishment of the newest arrivals (Crocker and Major 1955, Yarranton and Morrison 1974, Connell and Slayter 1977).

At an even smaller scale, the clonal growth strategies described by Lovett Doust (1981) convey two means of movement. The phalanx growth strategy, which is characterized by high aggregation of ramets, and the guerilla growth strategy, with a more loose spatial arrangement of stems, imply that ramets are capable of both spatially restricted, and widespread movement.

In another type of population movement, the spatial extent of a population may remain static, but the arrangement of individuals within it can change. This is the central idea behind the relatively recent concept of species mobility. Proposed as a way to explain species coexistence and high diversities, species mobility is a combined description of stem frequency in space, and in time, and is supposed to characterize species turnover, by how quickly new individuals establish, fulfil their life cycle and disperse their seeds (van der Maarel 1996). Klimes (1999) suggested that species with a fast turnover, change neighbours frequently in such a manner that individuals are sometimes situated beside a superior resource competitor, and at other times beside an inferior resource competitor. Over a long period of time, this can reduce the effects of superior competitors on inferior species.

Based on a species' frequency in space and variability in time, van der Maarel (1996) suggested five classes of mobility (Table 1-1). Thus, unlike the clonal growth strategies which are characterized strictly by the spatial configuration of stems, species mobility has an explicit temporal aspect, measured by monitoring the presence of species in quadrats over a period of time. Such temporal information is necessary for examining population

Table 1-1. Five classes of species mobility characterized by stem frequency in space and in time, as described by van der Maarel (1996). Frequency in time can also be viewed as inversely related to the variability of species presence in time.

Class Name	Frequency in Space	Frequency in Time	Description
Occasional	low	low	- usually present somewhere but change position
Local	low	high	- infrequent but remain in the same plots
Constant	high	high	- occur everywhere and at all times
Pulsating	medium	low-medium	- absent for long periods followed by periods of high frequency
Circulating	medium	medium-high	- frequent but do not remain in the same place from year to year

movement.

These perspectives of plant population movement, which are not exhaustive, depend very much on scale. For example, species mobility examines plant movement within the spatial extent of a population. The view of plant population movement taken in this thesis is somewhat different, involving the expansion, or colonization and establishment in new territory. As pioneering works in sand dunes and receding glaciers have shown, this type of movement is intrinsically associated with plant community succession, regeneration and development (Crocker and Major 1955, Yarranton and Morrison 1974).

Other evidence of such movement can be seen from patterns of plant age in space. For example, Barnes (1966) noted clonal expansion in aspen (*Populus tremuloides* and *Populus grandidentata*) from the progressively smaller stem sizes that occur at increasing distance from a clone. Similar changes in stem age over a spatial interval have been found in the wave-regenerating high-altitude *Abies balsamea* forests (Spruegel 1976). In this case, a disturbance mechanism moves through space, as ice and wind-shear erode a forest edge. This edge moves downwind, with regenerating forest following at a similar pace. Other instances of plant movement can be seen at a grassland forest interface (e.g. Bazzaz 1996) where higher tree densities occur closer to a forest edge and seed source. Pelton (1953) gives another example. *Symphoricarpos occidentalis* is a clonal species with long-lived rhizomes which appear to expand radially. Although periodic fire removes the above-ground biomass, and perhaps the species' major competitors, the below-ground rhizomes often survive to expand the area occupied by the clone.

Although plant population movement at this scale is easily observed, does it convey

any novel information about population or community dynamics? If so, how should it be examined or quantified? Obtaining answers to these questions is the major goal of this thesis. To start, I address the second question by examining ways of describing plant population movement. I then go on to address the first question by using knowledge of species' dispersal and survival strategies to predict stem plant establishment patterns.

Measuring plant population movement

To examine movement or expansion of a plant population, the spatial and temporal locations of all individuals should be considered. The arrangement of these individuals is often non-random, and the non-random arrangement of things in space, is said to be spatial pattern. Spatial patterns come as two general types. Clustered or clumped patterns occur where individuals are typically found together, and “regular” or over-dispersed patterns occur when individuals are typically found away from each other. One way of looking at these two types of patterns is to say that individuals are associated with either the presence, or absence, nearby of other individuals.

Clustered and regular patterns each occur at opposite ends of a spectrum/continuum. The reference pattern that divides the spectrum and separates patterns into each group is randomness. Randomly associated individuals are independent of each other, and arrangements in which more stems are found together than expected from randomness are said to be clustered, and arrangements in which less stems are found together than expected are considered over-dispersed.

The scale of pattern is also important: objects like plants, can be clustered into patches at one particular scale, regular at a larger one, only to be clumped into super-patches at still a larger scale (Figure 1-1). The distribution of galaxies in the observable universe, for example, which themselves are clumps of stars and matter, are known to occur in clusters, and at a larger scale these clusters are known to clump, forming superclusters (Gregory and Thompson 1982). Spatial pattern is also not restricted to within a single class of objects, but can also be bivariate, i.e. between two types (e.g. Kershaw 1960, Dale and Powell 1994). For example, it may not be surprising that the spatial distribution of grazing ungulates is positively associated, or "aggregated" with grass species and grassland communities, and negatively associated, or "segregated", from trees and forests.

If spatial pattern describes the dispersion of things in space, then spatio-temporal pattern describes the arrangement among things in space and time. Spatio-temporal pattern can also be either clustered or regular. For example, when more plants are separated by a particular space and time interval than are expected when they are randomly distributed at any place and any time, then these individuals may be said to be clustered in space and time. Such pattern might even indicate a rate of population movement. This idea is addressed in Chapter 3, where a creeping habit of the clonal species *Populus balsamifera* is examined, from the age and spatial distribution of ramets along a transect.

There are many approaches to both spatial pattern analysis (cf. Cressie 1991), and spatio-temporal pattern analysis (cf. Cliff and Ord 1981), but one of the simplest is to examine nominal data, like presence/absence of individuals, in a spatially discrete grid, using

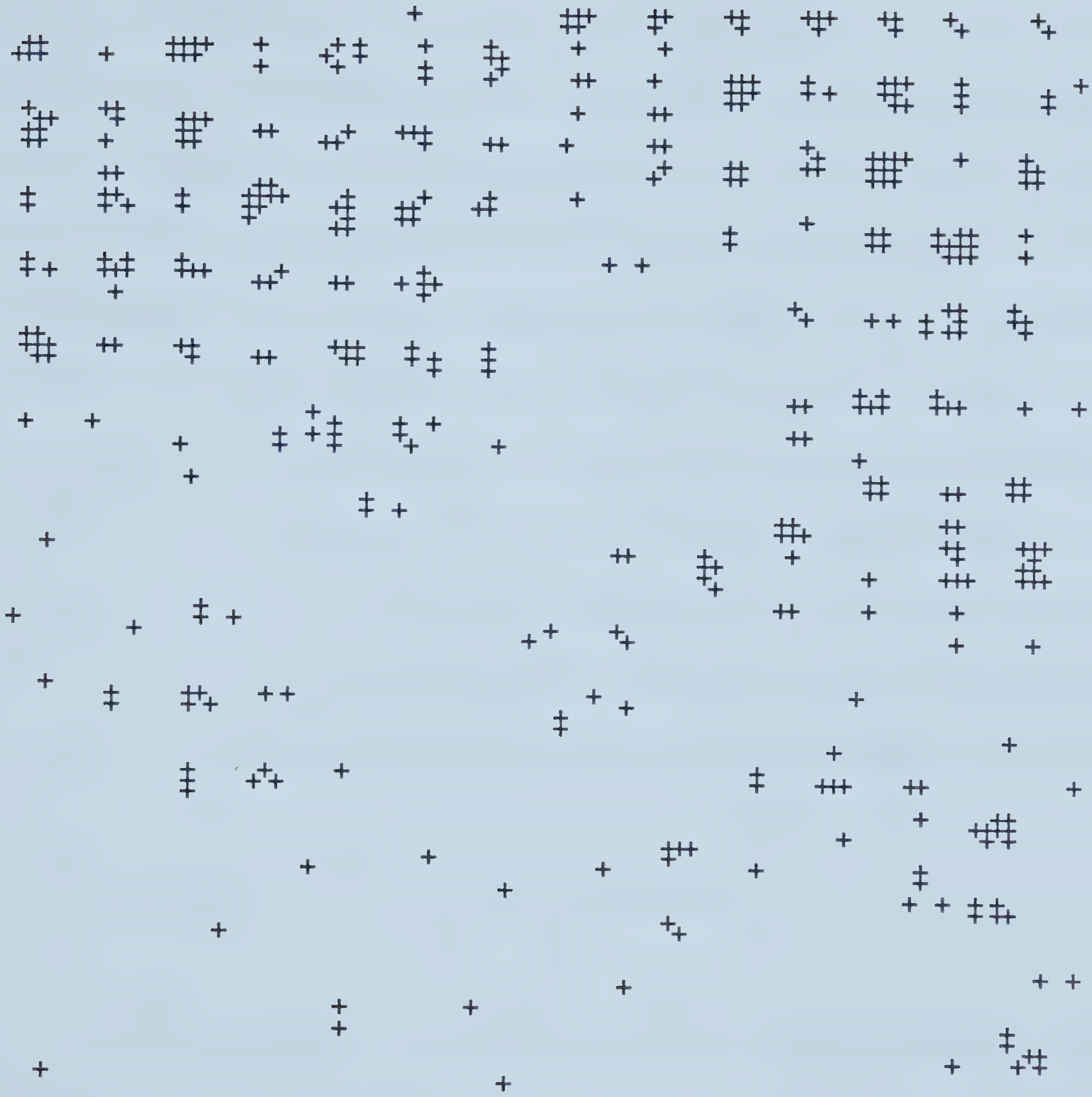

Figure 1-1. Spatial pattern where points are clustered at the smallest scale. At a slightly larger scale, the clusters of these points are regularly arranged, and at a still larger scale they are clumped toward the top of the figure.

join count statistics (Moran 1947, 1948, Sokal and Oden 1978, Cliff and Ord 1981). Join count statistics is a method that determines the number of times a particular interval separates pairs of individuals, compared to the number expected when individuals are arranged randomly. Pairs of individuals are connected by joins characterized by length (Figure 1-2) in either space, or in space and time. The first part of this thesis examines join count statistics as a way of analyzing for spatio-temporal pattern. First, join count statistics and the application to spatio-temporal pattern analysis are developed, and certain statistical aspects of join count statistics are explored. The approach is then tested on simple artificial and simple field data. Lastly, join count statistics are examined in greater depth, using more complicated data. Problems with the approach are discussed, the application of join count statistics to spatio-temporal pattern analysis is re-evaluated, and solutions are proposed.

Using spatio-temporal information on plant establishment

In the second part of this thesis I try to use spatio-temporal pattern to answer questions about biological processes. One of the original goals of this thesis was to determine whether post-fire boreal forest trees colonize from the edge of a disturbance area, or regenerate mainly from within. The basis of this was Rowe's (1983) convenient classification of boreal forest regeneration strategies, in which plant species were characterized as either invaders, evaders, avoiders, resistors or endurers. My interest focused on endurer and avoider species. Endurer, or phoenix species are those that re-sprout after the passage of fire, whereas avoider species are those that are usually listed as "species occupying unburned areas" (Rowe

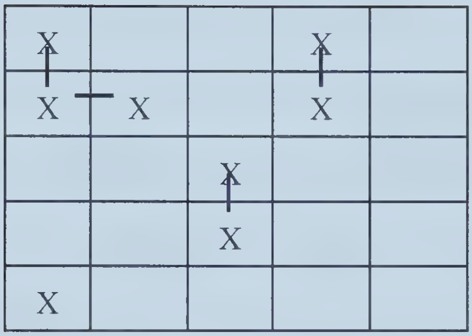

Figure 1-2. A grid containing nominal, binary, data where each cell has value "X" or is blank. All joins of one cell length that connect cells with X's are also shown (based on Sokal and Oden , 1978).

1983) and so must come from outside the disturbance area. In particular, I was interested in the degree to which "avoider" species slowly re-invade burned areas compared to "endurer" species, which re-establish the area occupied before the fire. My reasoning for using spatial pattern to assess these strategies was as follows: if "avoiders" re-invade the disturbance area then they must cross a fire boundary, and so population expansion into a burned area might be shown in the spatio-temporal arrangement of trees stems at the disturbance edge. Because stems are more likely to establish in areas close to the edge than areas farther away, in general these areas would be colonized first, and contain the oldest stems. I chose to examine trees because the year of establishment could be estimated from annual rings.

In general, establishment patterns were expected similar to those found by Bazzaz (1996) at a forest-grassland interface, which showed decreasing density of tree seedlings in a grassland with increasing distance from a forest edge.. With spatio-temporal information of tree establishment at the disturbance edge, I was also determined to measure the rate at which stems progressed into the disturbance area. The importance of these vegetation dynamics, I believed, was that the species composition in the areas surrounding the disturbance could prove very important as colonization occurred from the edge, enclosing the disturbance area.

Things were not that simple. Fire edges were hard to find, mainly because fire damage was so heterogeneous, and no area seemed to have the high degree of re-invasion coming from outside that was expected. However, most unexpectedly, but not surprising with hindsight, was that most regeneration appeared to come from within the fire boundary.

As in the first half of this thesis, where the use of join count statistics forced me to

re-evaluate what I thought of spatio-temporal pattern, the lack of colonization from outside the disturbance area forced a re-evaluation of what I thought post-fire establishment patterns in space and time meant, and how I should use spatio-temporal pattern analysis. So, combined with the idea that the initial species composition (Egler 1954) is the most important biological factor for recovery of post-fire boreal forest (Heinselman 1981), I re-focused tree stem establishment away from the disturbance edge, and on the initial establishers. The idea was that two principle species characteristics, dispersal and shade-tolerance, have great influence where and when stems establish relative to the initial establishers. My intent was to determine whether the pattern of establishment corresponded to species regeneration strategy, and to determine the relative importance of dispersal mode and shade-tolerance in post-fire recovery.

From examining post-fire establishment, this finally led to investigating the role of different processes that operate after establishment, and the patterns they make. Young plants are most often spatially clustered, either because resources, e.g. water, are aggregated, or because offspring are aggregated about parents, and many seedlings originate from a single seed cone or pod. Such spatial clustering, however, leads to intense competition, and so in places of post-fire boreal forest where species are initially clustered, intraspecific competitive relations are expected to predominate. As establishment was examined with respect to the initial establishers, so competition among the initial establishers was also examined. Thus, spatial patterns of one or more species were used to test whether intraspecific relations are more important than interspecific relations, as expected in a post-fire recovery period.

Conclusion

In the end, my idea of population movement in post-fire boreal forest trees changed somewhat, from a view centred on an expanding or encroaching vegetation interface like a disturbance edge, to a view centred on phoenix species re-establishment. This latter perspective is a more internal view of plant population movement, resembling the concept of species mobility. With the research that follows and the work of others that is currently being done, I believe that the idea of movement in plant populations is becoming clearer along with its importance, because although plants may indeed "stand still to be counted" as John Harper appreciated (Harper 1977), the same ones might not be there the next time you visit.

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CHAPTER TWO

BASIS FOR EXAMINING ASSOCIATION IN PLANT ESTABLISHMENT IN SPACE AND TIME: TWO-FACTOR JOIN COUNT STATISTICS

Introduction

The expected number of associations on a two dimensional random lattice was developed by Moran (1947, 1948) and Krishna Iyer (1949, 1950). Such a lattice consists of a random arrangement of different types of cells (e.g. black and white), and association is viewed as a join between two elements of predefined type or types (e.g. B-B or B-W). Joins are classified by length according to the number of cells traversed by either rook's, bishop's or queen's moves. Two types of random lattice can occur: either the probability of a cell type is constant (fixed p) or the number of cells of a specific type is constant (fixed P). In both cases, the probability distribution tends to normality as the size of the lattice increases (Moran, 1947, 1948). By obtaining the standardized normal deviate for each join length of an unknown lattice, Sokal and Oden (1978) showed that spatial distributions can be analyzed for non-random pattern. In plant ecology, for example, an $m X n$ lattice may describe the spatial distribution of a plant species in a two dimensional area, with black and white cells specifying presence and absence, respectively. The number of black-black joins of a specific join length that are observed, compared to the number expected from randomness, will

indicate either aggregated, random or uniform spatial pattern at that distance.

An m X n lattice may also depict a one dimensional transect of n quadrats at m different points in time. On this lattice, black-black joins between individuals are characterized by two factors, pertaining to a spatial interval s and temporal interval t. Association among plants on this lattice therefore is spatio-temporal, and comparison between the observed and expected number of joins in a particular class will indicate whether plants are aggregated, random or uniform in space and time.

Recently, in an effort to detect anisotropy in ecological spatial patterns, joins described by two-factor distance classes have been used, each factor pertaining to an interval in a spatial direction, (Proctor 1984, Gray et al. 1986, Dale 1995). The statistical tests employed have been based on contingency tables, (e.g. Proctor 1984, Dale 1995), or randomization tests (e.g. Gray et al. 1986). For large lattices, however, randomization tests can be time-consuming. Therefore, in this chapter, I determine the equations, in the fixed p case, of the first and second moments for the number of two-factor joins on a randomly arranged lattice.

Random Association of Black Cells on a Lattice

Consider an m X n lattice or grid of black and white cells and let the probability that cell, x_{ij}, is black be $pr(x_{ij}=B)= p$, where $1\leq i\leq n$, $1\leq j\leq n$. In the fixed p case, the probability of choosing a second black cell is the same, and so the probability that any two cells are black i.e. the probability of a black-black join, is, $pr(x_{ij}=B,x_{kl}=B)= p^2$. Letting $x_{i,j}$ =1 if black and 0 otherwise, based on Moran's (1947) work with single factor joins, the number of two-factor

joins of class (s, t) on the lattice can be defined as,

$$Q(s,t) = \sum_{i=1}^{n-s}\sum_{j=1}^{m-t} x_{i,j}\, x_{i+s,j+t} + \sum_{i=1}^{n-s}\sum_{j=1}^{m-t} x_{i+s,j}\, x_{i,j+t} \qquad (1)$$

where $s>0$, $t>0$. From (1) there are $2(m-t)(n-s)$ possible joins and therefore the number of joins expected among randomly distributed black cells is,

$$E(Q) = (2mn - 2nt - 2ms + 2st)\, p^2 .$$

The derivation of the second moment $E(Q^2)$ is similar to Moran's (1948). First let $g_{ij}=x_{ij}\, x_{i+s,j+t}$ and $h_{ij}=x_{i,,j+t}\, x_{i+s,j}$ so that

$$Q = \sum_{i=1}^{n-s}\sum_{j=1}^{m-t} g_{ij} + \sum_{i=1}^{n-s}\sum_{j=1}^{m-t} h_{ij}$$

and so,

$$Q^2 = [\sum_{i=1}^{n-s}\sum_{j=1}^{m-t} g_{ij} + \sum_{i=1}^{n-s}\sum_{j=1}^{m-t} h_{ij}\,]^2 = (\, g_{11} + g_{12} + \bullet\bullet\bullet + g_{n-s,m-t} + h_{11} + h_{12} + \bullet\bullet\bullet + h_{n-s,m-t}\,)^2 . \; (2)$$

By expanding (2), the expected value of Q^2 is the sum,

$$E(\, Q^2\,) = E(\, g_{11}^2\,) + E(\, g_{11} g_{12}\,) + E(\, g_{11} g_{13}\,) + \bullet\bullet\bullet + E(\, h_{n-s,m-t}\, h_{n-s,m-t-1}\,) + E(\, h_{n-s,m-t}^2\,). \qquad (3)$$

This equation has $(2mn-2ms-2nt+2st)^2$ terms, each corresponding to one of three ways that two joins may associate. For example, the first type of term describes two joins that

share two cells (e.g. g_{11}^2 and h_{11}^2). Each of these has an expected value, $E(g_{ij}^2)= E(h_{ij}^2)= p^2$, and there are $(2mn-2ms-2nt+2st)$ of them.

The second type of term in the expansion of Q^2 are those products of g_{ij} and h_{ij} that correspond to two joins sharing a common cell (e.g. $g_{ij}\, g_{i+s,j+t}$ or $g_{ij}\, h_{i+s,j}$) and each has an expected value, $E(g_{ij}\, g_{i+s,\, j+t})=p^3$. To determine the number of these terms, consider all of the g_{ij} joins, for i=1 to s, j=1 to t (Figure 2-1): there are st of them, and each can share one cell with only 3 other joins (e.g. join A Figure 2-1). Therefore, for these g_{ij} there are $3st$ pairs of joins that share only one point. The result is the same for h_{ij} joins, where $i=n-2s+1$ to $n-s$, $j= m-2t+1$ to $m-t$. Figure 2-1 shows that joins in other parts of the lattice can share a single cell with 2, 4 or 6 other joins (not shown), and based on this, the total number of join pairs that share one point is, $2[2(3st)+2(2st)+2\{4s(m-3t)\}+2\{4t(n-3s)\}+6(m-3t)(n-3s)]=12mn-20ms-20nt+32st$.

The third type of term in the expansion of Q^2 are those products of g_{ij} and h_{ij} that share no common cell (e.g. $g_{11}g_{13}$). The expectation of these terms is, $E(g_{ij}\, g_{kl})=p^4$, and they are counted by subtracting the total number of the previous two terms from all join pairs that are possible. By summing the expectations of each type of term, the second moment, $E(Q^2)$ is,

$$E(Q^2) = (2mn - 2ms - 2nt + 2st)\, p^2 + (12mn - 20ms - 20nt + 32st)\, p^3$$

$$+ [(2mn - 2ms - 2nt + 2st)^2 - 14mn + 22ms + 22nt - 34st]\, p^4 . \quad (4)$$

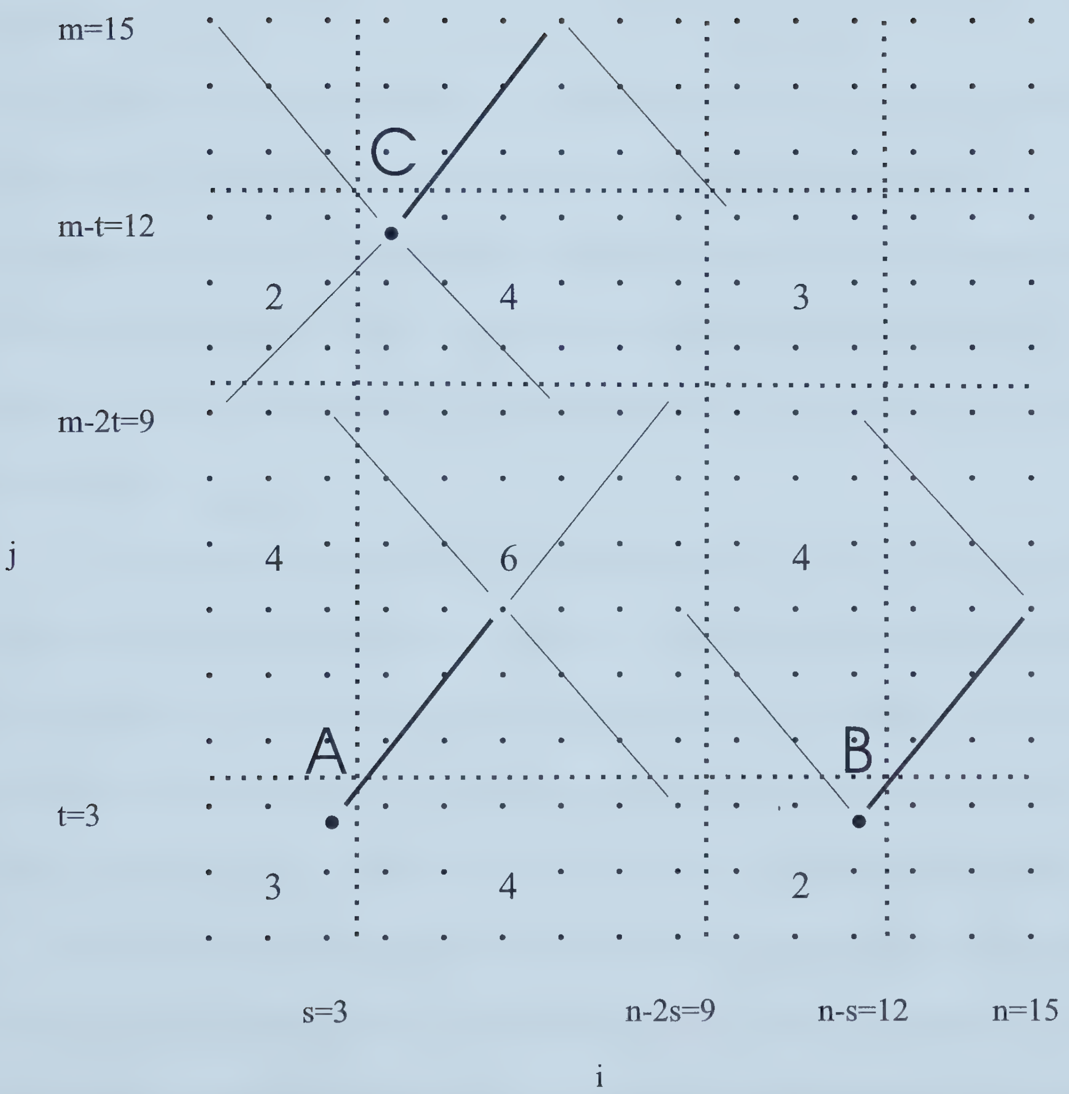

Figure 2-1. A subdivided (15X15) lattice. The number of companion joins with which g_{ij} joins of class s=3, t=3 share a single cell is indicated by the number in the respective subdivision. For example, join **A**, or g_{33} may share a single cell with three other joins. Join **B**, $g_{12,3}$, can share a single point with two other joins, and join **C**, $g_{4,12}$, with four other joins.

Figure 2-1 shows also that (4) is conditional on $s \leq n/3$ and $t \leq m/3$. For other values of s and t, the second moment can be similarly calculated.

Conclusion

Table 2-1 shows the mean and variance for selected two-factor join classes on a 10X10 random lattice. These values are close to those derived from 1000 iterations of a randomly arranged lattice. The probability distributions generated by randomization are skewed for small values of m and n (not shown) but become more bell-shaped with increasing lattice size and so the use of standardized normal deviates should be restricted to large lattices .

Calculating the moments for two-factor associations of points on a large random lattice offers an alternative to the use of contingency analysis and randomization models, for the detection of anisotropy in spatial patterns. As analysis of single factor associations for different distance classes gives a two dimensional correlogram (Sokal and Oden, 1978), analysis of two-factor associations will create a three dimensional correlogram.

Two-factor associations can also be used to examine spatio-temporal pattern. This is done in the next chapter where a spatio-temporal lattice is made by mapping trees and counting annual growth rings. Black cells on a lattice represent establishment of a stem in a particular quadrat, at a particular time, and spatio-temporal association among stems are examined with two-factor join count statistics. A large value for a particular association means that more joins of length (s,t) were observed than were expected from randomness.

Table 2-1. The mean and variance for four selected two-factor (s,t) join classes on a 10X10 random lattice, *p*=0.2, and the statistics calculated from 1000 iterations of each random model.

Join Class		Equation		Randomization	
s	t	E(Q)	var(Q)	E(Q)	var(Q)
1	1	6.48	11.55	6.77	12.94
1	2	5.76	9.78	5.89	9.99
2	1	5.76	9.78	5.89	9.72
2	2	5.12	8.29	5.20	8.21

Under certain circumstances, this can be interpreted as a rate of colonization where plants take on average *t* years to colonize areas *s* quadrats away.

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CHAPTER THREE

A METHOD FOR ANALYSING SPATIO-TEMPORAL PATTERN IN PLANT ESTABLISHMENT: AN EXAMPLE FROM A *POPULUS BALSAMIFERA* CLONE

Introduction

It has long been evident that ecological spatial patterns change in time, often in predictable ways (Watt 1947, Andrewartha and Birch 1954, Hanski 1996). Spatio-temporal pattern is the tendency for non-random association (either positive or negative) between events separated in space and time. For example, consider a string of light bulbs where one light blinks, and in the next moment the one to its immediate left does the same. Blinking does not occur randomly at any place and time, but is associated with the blinking of a neighbouring bulb.

In plant ecology, the concept of spatio-temporal pattern goes back at least to Watt (1947) who recognized that different vegetation phases tended to be close in space and time. More recently, Herben, During and Krahulec (1995) examined species abundances across permanent plots over a period of nine years and showed that species' densities change predictably at different places and times, relating this pattern to clonal growth form.

Clonal growth forms have been described by the spacing of ramets (e.g. Lovett Doust 1981). Under certain circumstances, however, the distribution of stem establishment in space and time may better describe them. For example, a “phalanx” growth strategy, characterized by compact spatial structure of ramets (Cheplick 1997), would display highly predictable

stem establishment in space and time, as stems either advanced to increase the size of the patch, or remained static, to defend it (Slade and Hutchings 1987). The guerilla form, characterized by more loosely arranged ramets, could show either more unpredictable stem establishment in space and time, as the military metaphor suggests, or it could show highly predictable establishment. Because both growth forms can be thought of as the endpoints of a continuum (Cheplick 1997), such clonal growth forms can be classified or quantified based on two aspects, the spatial arrangement of ramets, and predictability of ramet establishment in space and time (cf. Oborny 1994).

Methods used to elucidate spatio-temporal pattern have generally extended single factor autocorrelation analysis to two factors or lags, each pertaining to an interval along a spatial axis and a time axis (e.g. Herben et al. 1995). Griffith's Space-Time Index, for example, is related to Moran's I, but examines the value of a variable at different places and times (Henebry 1995). It is applied to interval variables such as plant density. If, however, presence/absence of individuals is considered, then analysis of such a binary variable involves the statistics of join counts (Cliff and Ord 1981).

Recently, two-factor join count statistics have been used to detect anisotropy in ecological spatial patterns, each factor pertaining to a specified interval in a spatial direction (Proctor 1984, Gray et al. 1986, Dale 1995). To my knowledge, two-factor join count statistics have not been used for analysing spatio-temporal patterns in plant ecology. This approach may prove informative because it deals explicitly with individual plants. This chapter demonstrates a two-factor join count approach by focusing on the establishment of individuals in space and time. Field and artificially generated spatio-temporal data are

analysed.

Artificial arrangements were analysed to determine the extent that non-random pattern can be distinguished when noise is added. A field site was chosen where spatio-temporal pattern was evident. This occurred at the interface of a forested area and grassland, where clonal *Populus balsamifera* L. ramets were seen to decrease in size with increasing distance from the forest, forming an advancing front of establishing ramets. I not only show clonal movement along a transect, but also determined the rate of movement of ramet establishment, as defined above. I relate this to clonal growth strategies, and show that spatio-temporal pattern of plant establishment, described by two-factor join count analysis, can provide a means of quantifying clonal growth strategy.

Methods

Join count statistics are a way of measuring autocorrelation in nominal data distributed across a lattice or grid (Cliff and Ord 1981). Because I deal specifically with binary data, each cell of a lattice takes one of two values, black or white, representing presence or absence. Autocorrelation among cells compares the number of joins in an observed data set to number expected when the cells are randomly arranged. A join is a connection between pairs of pre-defined types of cells (e.g. black-black) separated by either rook's, bishop's or queen's moves, and is further classified by length as the number of cells traversed (Sokal and Oden 1978). On a two dimensional lattice representing a spatial area, if the observed number of black-black joins of length class *d* is greater than expected, then black cells are said to be positively autocorrelated at distance *d*. Where the observed number is less than expected, black cells

are said to be segregated or negatively autocorrelated at distance *d*.

In a two-factor spatio-temporal approach, however, a two dimensional lattice represents a single spatial dimension, (e.g. a transect of *n* quadrats) at *m* intervals of time. This represents a time sequence of a one dimensional transect, with each cell specifying a particular place along it at a particular time. Black cells on this lattice signify plant establishment rather than presence *per se* because establishment represents a more brief event than presence, and several differently aged plants in a quadrat (i.e. column of the lattice) can be distinguished by multiple black cells in it.

On a spatio-temporal lattice, join lengths are specified by a combination of two factors (s,t), each pertaining to an interval along an axis, and no distinction between negative and positive joins is made. For example, join class (2,3) signifies joins of length 2 units along the spatial axis and 3 units along the time axis. Each pair of black cells is connected by a join, and spatio-temporal association among establishment events is examined by comparing the observed number of black-black joins of several join classes to the number expected from randomness. The results can then be displayed on a correlogram in which two axes comprise the join combinations and a third the autocorrelation statistic. The autocorrelation statistic is expressed as the deviation of the observed number of joins from expected. If more joins occur than are randomly expected then there is a tendency for stems to be separated by s spatial intervals in t time units. This gives a measure of colonization rate.

Plant ecologists may not be interested in all stems that establish in each quadrat, but rather only in the first. Concentrating only on the initial establishers would give information on population expansion, and would reduce the number of associations among young

individuals that establish profusely but are unlikely to survive. The spatio-temporal arrangement of the initial colonizers is, therefore, represented as a lattice with at most one black cell in each column. To compare such a spatio-temporal arrangement to what is expected from randomness, I consider two other ways, or models, in which black cells can be randomly arranged so that no more than one can occur in a column (i.e. in one quadrat). First, a quadrat has probability r, that it is colonized, i.e. the probability that a column contains a at least one black cell is r, and each black cell that occupies a column is distributed uniformly among rows. I call this type of random lattice the "uniform row" model. Alternatively, black cells may occur in any cell on the lattice with probability p, but only those in the highest row of each column (i.e. the earliest establisher) are retained. This second random lattice I term the "top-black" model because only the "highest" black cells, i.e. the oldest, in a column, are retained. Both of these models are distinguished from the "fully randomized cell model" where more than one black cell may occupy a column, and the probability of any cell being black is p.

In order to examine spatio-temporal pattern among all stems, and among the initial colonizers in a quadrat in this paper, the number of joins expected from randomness was determined according to one of the three random models (i.e. fully randomized cell, uniform row or top-black). For each, 10 000 random lattices per join class were generated, and from these obtained a frequency distribution, $f(Q_{st})$, and expectation, $E[Q_{st}]= \Sigma Q_{st} f(Q_{st})/10000$, where Q_{st} is the number of joins, Q, in join class (s,t). An alternative approach would have been to generate 10 000 random lattices per analysis and obtain a frequency distribution for all join classes from all of these random lattices. I chose the former approach, however,

because join classes are not independent of each other, e.g. two join classes of (1,1) will give one join class of (2,2), and so in order to perform an accurate statistical test for each join class, separate randomization procedures should be used for each.

The autocorrelation statistic of each join class was based on the deviation of observed from expected join frequencies. Deviations were calculated by allocating each observed count to a tail of $f(Q_{st})$ on either side of $E[Q_{st}]$. This was assigned a percentile value based on the number of randomly generated lattices remaining in the tail (equivalent to a one-sided hypothesis test) and was expressed as a *P*-value. Two-factor correlograms depicted each join class on an array of circular cells, with *P*-value as circle area.

Populus balsamifera ENCROACHMENT DATA AND ARTIFICIAL DATA

Four 15 x 15 lattices were created as artificial spatio-temporal arrangements. The purpose for using them was to determine whether join count statistics could reveal data that contained known pattern. The first artificial lattice, A, was a random or null lattice created by assigning black to each cell with a probability $p = 0.2$. The second artificial lattice, B, is analogous to a string of blinking lights, and comprised a black cell every $s = 1$, $t = 1$ interval on the lattice starting in the top right corner (not shown). The last two artificial arrangements were variations of artificial lattice B, but two types of noise were added. In artificial lattice C, random background noise was added by including black cells not in the pattern of B, with probability 0.10 (Figure 3-1a). In the fourth artificial lattice, D, each black cell in pattern B was randomly shuffled among time intervals according to the integer component of the

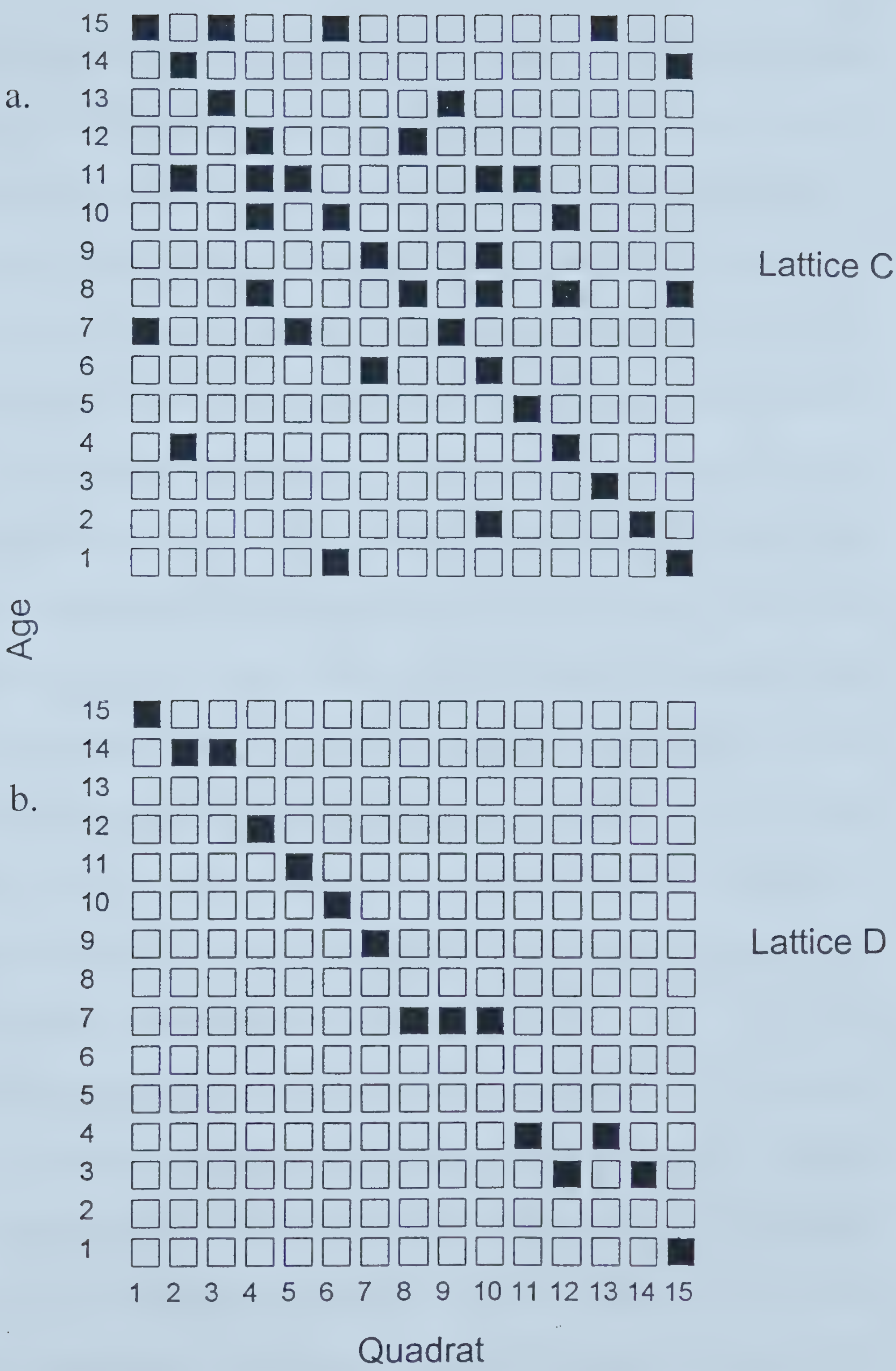

Figure 3-1. Artificial spatio-temporal pattern consisting of variations on lattice B (not shown) **a**. lattice C, 10% background noise and **b**. lattice D, shuffled pattern. Black cells represent establishment.

Gaussian random variable, *N(0, 0.5)*, (Figure 3-1b). For example, if the value of a Gaussian random variable is -1.5 for the black cell in the top left corner of Lattice B, then a black cell in the new lattice, D, will occur -1 time intervals away from the black cell in lattice B.

Field-based spatio-temporal arrangements were examined at the Ministik Bird Sanctuary southeast of Edmonton, Alberta, Canada. This area contains forest patches, generally greater than 1 ha, set amongst a mowed grassland. Patches consist primarily of white spruce, *Picea glauca*, and balsam poplar, *P. balsamifera*. In some areas, mowing at the edge of these patches has ceased and the species are colonizing the grassland area. An area of *P. balsamifera* colonizing activity was selected, and three belt transects 1 m wide and up to 13 m long were extended from a patch edge into the grassy. Stems were mapped to within 0.5 m intervals along these transects, cut, labeled and then age was determined by ring counts in the laboratory. Aging consisted of sanding a stem cross-section with 120 grit sand paper on a belt sander. Hand sanding was done with 150-220 grit sand paper, and rings were counted under a dissecting microscope. The resulting data gave three lattice representations of the spatio-temporal arrangement of ramets (Figure 3-2).

More complex data were obtained from *Populus tremuloides* in two 150 m transects in a 21 year old boreal forest post-fire area near Wandering River, Alberta. This site appeared to contain a fire edge caused by a fire break or seismic line, and within the disturbance area an open canopy of *P. tremuloides*, approximately 5 m in height, occurred along with *Picea mariana* below 1 m in height. Outside of the disturbance area large *P. mariana*, and *P. tremuloides* were approximately 10 m high. Because these data were collected before the data at Ministik, a larger spatial scale of 1 m^2 transects was used. As at Ministik, however,

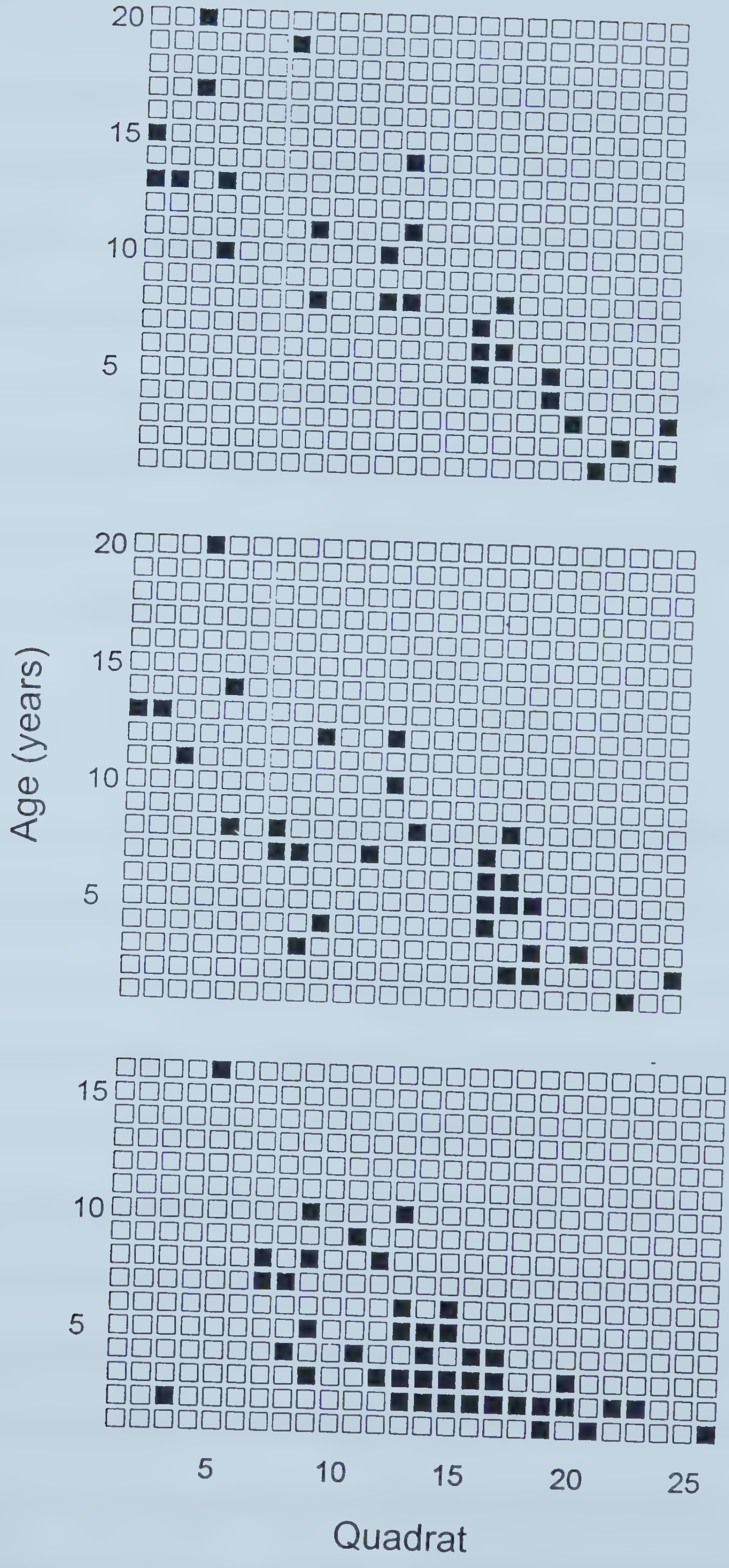

Figure 3-2. Lattice representation of spatio-temporal arrangements of *P. balsamifera* along three transects, at Ministik Bird Sanctuary, Alberta, Canada. Black cells represent establishment. Quadrats represent 0.5 m spatial intervals.

all of the tree stems in a quadrat were cut and age was determined in the laboratory.

For analyses using the uniform row and top-black models, the observed spatio-temporal lattices were manipulated by deleting all occupied cells in a quadrat (column) except the first to occur (i.e. the top-most, i.e. oldest, black cell). In the fully randomized cell and top-black models, the proportion of black cells on the observed lattice were used as an estimate of p, the probability that black cells occur in the random model. In the uniform row model, the number of occupied quadrats on the observed lattice were used to estimate r, the probability of an occupied quadrat on the random lattice.

Results

Analysis of the random artificial lattice, A, using the fully randomized cell model showed only small deviations from expectation for all join classes. After deleting all but the top or first occupant of each column, analysis using both uniform row and top-black models also showed small deviations from expectation. To save space, these simple results were not shown. Analysis of the artificial lattice B, where $s = 1$, $t = 1$, showed a large excess of joins in class (1,1), (Figure 3-3a). Large resonance deviations occurred at multiples of this class, e.g. (2,2), (3,3). The uniform row and top-black models showed similar results (not shown).

When this pattern was obscured with 10% background noise (Figure 3-1a), the pattern was detected using the fully randomized cell model (Figure 3-3b), but the P-value of join class (1,1) and subsequent resonance peaks were smaller than when the pattern was without background noise (Figure 3-3a). When the pattern is jumbled to produce lattice D, (Figure 3-1b), two-factor join analysis using the fully randomized cell model found a large

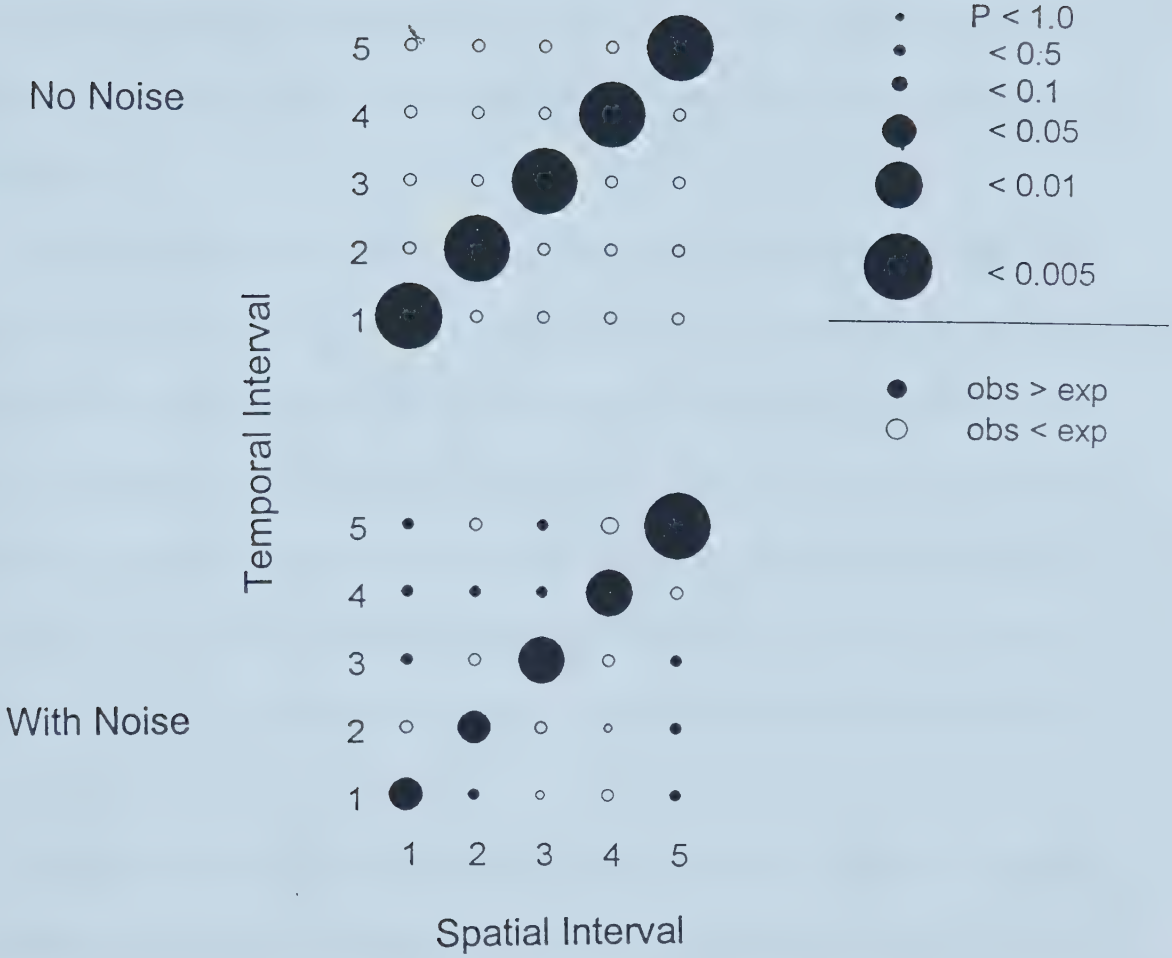

Figure 3-3. Two-factor correlograms for the analysis of **a**. lattice B (no noise) and **b**. lattice C (with noise), using the fully randomized cell model for each join class, black circles represent positive autocorrelation, and white circles negative. Circle size indicates *P*-value.

positive deviation at the original pattern (1,1), and smaller resonance peaks at multiples of the pattern (Figure 3-4a). Similar results were found by the uniform row and top-black models, but the deviations were larger (Figure 3-4b and c). In general, as would be expected, when the variance of the shuffling procedure is increased and black cells deviate more from the original (1,1) pattern, there is a corresponding greater difficulty in distinguishing the original pattern.

Analysis of the three transects of *P. balsamifera* clonal colonization using the three random models is shown in Figure 3-5. In the first transect, analysis using the fully randomized cell model showed large positive deviations at join classes (1.5, 2), (2.0, 2), (1.5, 3) and (2.0, 3) (Figure 3-5a). A peak also occurs at (3.5, 5). This is interpreted as a resonance peak because it is exactly twice the value of the middle of the smaller four adjacent peaks, centred at (1.75, 2.5). Analysis using the uniform row and top-black models were similar. Each showed a peak at (2.5,6) (Figure 3-5b and c), and only the uniform row model had a peak at (1.5, 2).

In the second transect, a slightly different pattern was evident. Analysis using the fully randomized cell model gave large positive deviations at (0.5, 1), (0.5, 3) (2.0, 4) and (2.5, 5) (Figure 3-5a). Using the other two models, however, a large positive deviation occurred at (1.0, 2) (Figure 3-5b and c). Possible resonance peaks are apparent at (2.0, 4) and (2.5, 4) in the uniform row model. As in the first transect, these resonance peaks lend support to the conclusion that a pattern occurs at (1.0, 2).

Analysis of transect 3, with the fully randomized cell model showed large positive deviations for joins where $t = 1$ and $t = 2$ making interpretation difficult (Figure 3-5a). This

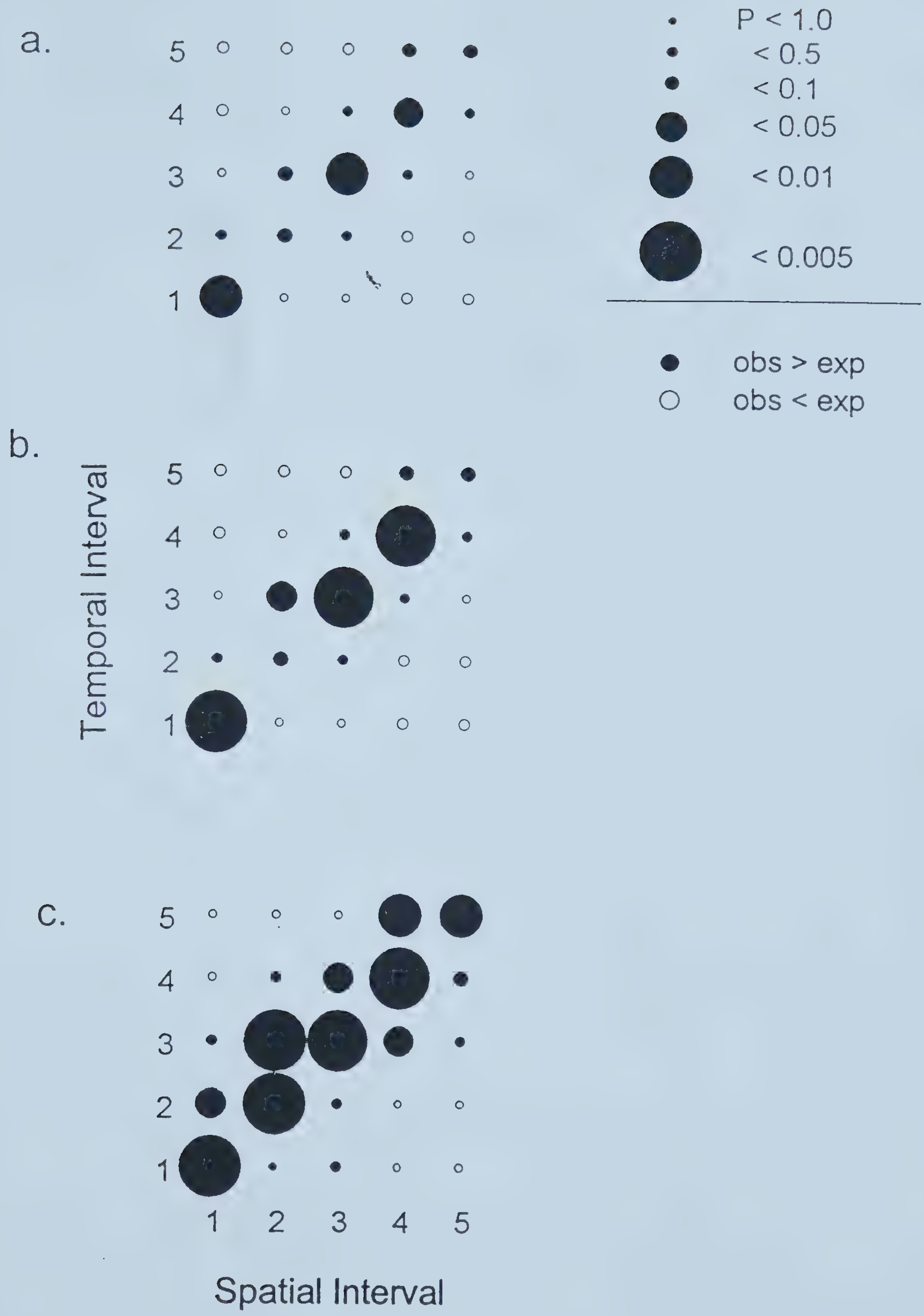

Figure 3-4. Two-factor correlograms for the analysis of artificial data lattice D (Fig. 3-1) using **a**. the fully randomized cell model, **b**. the uniform row model and **c**. the top-black model. For each join class, black circles represent positive autocorrelation, and white circles negative. Circle size indicates *P*-value.

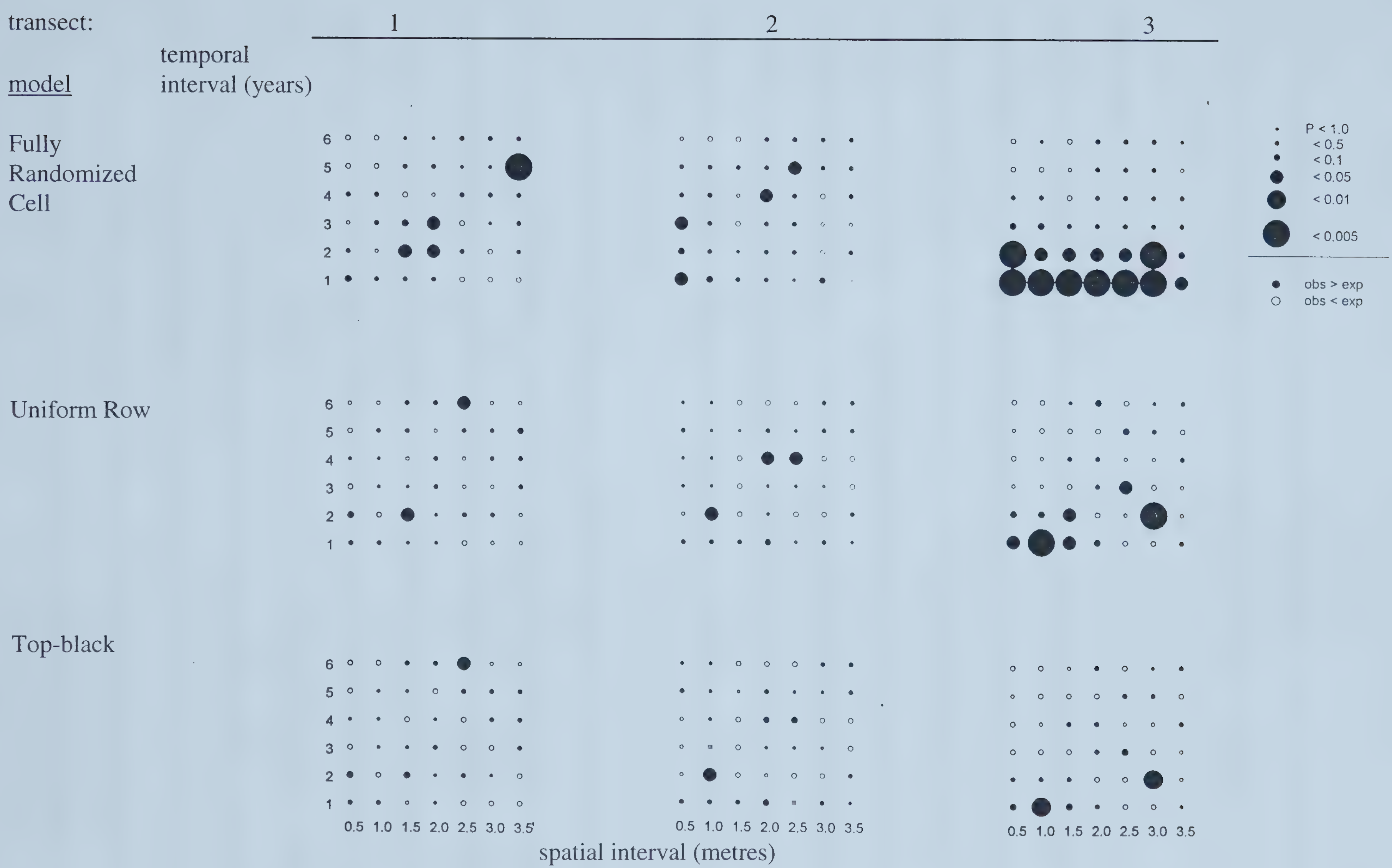

Figure 3-5. Two-factor correlograms of *P. balsamifera* spatio-temporal arrangement in the three transects, using the three random models. Black circles represent positive autocorrelation, and white circles negative. Circle size indicates *P*-value.

36

was the primary reason that the two other models were introduced. Analysis using these both showed large peaks at around (1.0, 1) and another at (3.0, 2) (Figure 3-5b and c).

Discussion

I have used a method that examines the association among stems established at different times and places, and have interpreted colonization rates in a *P. balsamifera* clone, averaging approximately 1.75 m in 2.5 years in transect 1, 1 m in 2 years in transect 2, and 1 m in 1 year in transect 3 (Figure 3-5). Another method of measuring colonization rate would be to fit a line to a lattice (e.g. Figure 3-2) and obtain rate from the slope. This method would give something comparable to 1 m in 1 year, but it would not test for random establishment, nor would it accurately characterize more complex patterns as when stems establish 2 m in 2 years, or as in Figure 3-6.

The lattice in Figure 3-6 represents a transect comprised of multiple vegetation patches that grow and eventually coalesce through time (e.g. Greig-Smith 1964, Yarranton and Morrison 1974, Dale and MacIsaac 1989). The major difference between this lattice and Figure 3-1 or 3-2 for example, is not the rate of establishment, but the spatial pattern in the initial time period. In the former, there is a regular pattern in every eight quadrats of the initial time period, but in the latter there is none. Initial spatial structure could be incorporated into the method presented here by including horizontal joins (i.e. join classes where $t = 0$). Horizontal joins represent spatial associations between stems of the same age, and so any spatial pattern in the initial and subsequent time periods, will be included in the analysis. Horizontal join classes were not included in the analyses because it appeared that

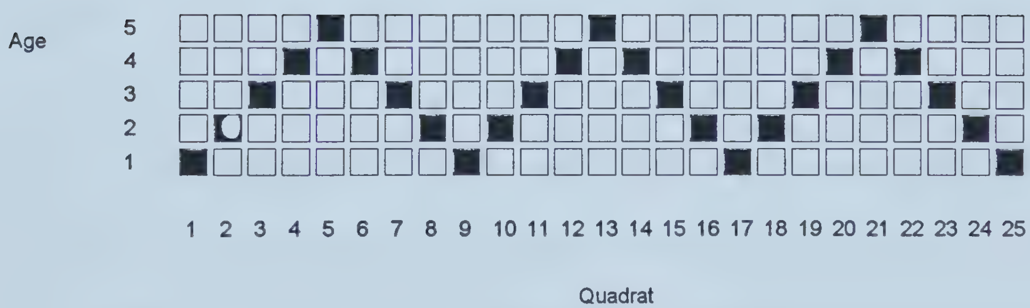

Figure 3-6. Hypothetical spatio-temporal arrangement of a transect in which 3 quadrats are initially colonized, and nucleate in both directions of the transect to eventually coalesce.

P. balsamifera were without this spatial structure.

In *P. balsamifera,* most reproduction is vegetative by root stems or suckers, and as Barnes (1966) visually documented in other *Populus* species, stem age at the field site decreased away from the centre of the clone. There are two possible explanations for this. First, lateral roots of the clone may have been present in the grassland before the last mowing. The difference among stem establishment times along transects, therefore, could be caused by a reduction in photosynthate translocated through the root system as distance from the clone centre increases, allowing closer stems to establish first. Although some evidence suggests that distance from parent tree is not a regulating factor, the relation between sucker development and the parent root system is not well understood (Peterson and Peterson 1992).

An alternative explanation is that ramet establishment followed root growth. Presumably, the clone is producing adventitious roots in the grassland to "forage" or escape a competitive environment. The higher soil temperature which stimulates sucker development and is experienced by adventitious roots as they enter this area could, therefore, result in sucker establishment following root growth (Peterson and Peterson 1992).

Spatio-temporal pattern of stem establishment could offer a way of quantifying clonal growth forms. The clonal growth form of *P. balsamifera* showed ramet establishment was highly predictable in space and time, i.e. spatio-temporal the clonal growth showed strong spatio-temporal pattern. High spatio-temporal predictability is due to there being little uncertainty as to where resources are. For example, light, an important limiting resource for the species (Peterson and Peterson 1992), is abundant in the grassland. The loose spatial

arrangement of colonizing ramets could be the result of a trade-off between allocating resources toward either lateral root growth, or sucker establishment, although most suckers originate on relatively small roots between 0.5 cm and 2 cm in diameter (Peterson and Peterson 1992). Similar, growth forms are apparent in post-fire *P. balsamifera* expansion (Brodie, Houle and Fortin 1995), and in the beachward advance of sand dune grasses, like *Ammophila breviligulata* (Maun 1985).

In field data collection, time of establishment was estimated from tree rings. The results should be interpreted with caution because I have assumed that the oldest observed stem in a quadrat was first to colonize, and that no mortality has occurred. This assumption would be violated if an initial colonizer is replaced by a late-coming, superior competitor.

Two-factor join count autocorrelation analysis discerned all non-random artificial data. As background noise was added, or the pattern was jumbled, this ability diminished. Resonance peaks occurred at multiples of pattern, and these helped confirm the character of pattern.

Interpretation of spatio-temporal pattern depended on the model used for comparison because each model produces a different random lattice. Nevertheless, the uniform row and top-black models were used to help distinguish pattern in noisy spatio-temporal arrangements, and were successful for two reasons. First, analysis using these models gave larger deviations than the fully randomized cell model, and larger deviations indicate that the analysis is better able to discern pattern. Second, analysis using these models reduced the large number of significant deviates that can result when using the fully randomized cell model. For example, the large number of significant deviates in transect 3, Figure 3-5a,

obscure any interpretation. The reason for this is a cluster of 2 and 3 year old stems in quadrats 12 through 20 (Figure 3-2c). Such clusters give more joins of class (0.5, 1) than are expected by the fully randomized cell model. This problem is alleviated, however, in the uniform row and top-black models by removing the cluster and operating only on the initial colonizer of each column. Although each model produced a slightly different result, both helped interpretation.

Observational scale, i.e. extent and grain size (Wiens 1989), affects pattern interpretation. The extent of a spatio-temporal investigation depends on both transect length, and the time elapsed since an initiating disturbance event, which is related to the size of the spatio-temporal lattice. The grain of scale, however, depends on quadrat size, quadrat spacing and the time interval between observations. Examination at relatively large spatial and temporal scales might best be accomplished using interval variables, like plant density, and Griffith's Space-time Index. At smaller scales, however, such as that of an individual plant, two-factor join count statistics can prove more useful. At these scales, I believe that spatio-temporal pattern of stem establishment provides a good descriptor of plant behaviour, and that a better understanding of plant stem interactions could result from considering patterns of establishment and mortality in both space and time.

Critique of join count statistics for measuring spatio-temporal pattern

Despite the results given by two-factor joins count statistics in a simple data set, when applied to more complicated data I do not believe that they are useful in the manner

that was initially hoped, because they indicate little more than peaks at low time and spatial intervals. For example, analysis of two 150 m transects in a 21 year old post-fire boreal forest site, only showed that stems tended to be separated by 1 or 2 years in age (Figure 3-7), and the Uniform Row Model did not greatly improve the results (Figure 3-8). There is an indication of similar results in transect 3 of the Minisitik data set (Figure 3-2), and there are two reasons why I believe this occurs. First, join count statistics assumes that stems occur with equal probability at all points in time. This is not a valid assumption because there is a greater probability of finding relatively young stems than old (Figure 3-2). Second, given that establishment in time can vary, another problem with join count statistics is that pattern or association among stems is analysed relative to other stems, and not to a fixed point in time, e.g. time of disturbance.

Although there are alternative methods to analysing spatio-temporal pattern (Cliff and Ord 1981, Henebry 1995), I believe that all should have the common characteristic that stem establishment is examined relative to a fixed point in space and time. In the remaining chapters, a relatively simple approach to this is taken, consisting of bivariate spatial association between two ages at a time. Although all ages are examined, they are all done so in comparison to one fixed set of stems, the oldest. In this manner, and unlike join count statistics, a surge and cessation of stem establishment can be seen in the amount and spatial association of different aged stems relative to the oldest ones.

Finally, to end this part, I have to question the importance of spatio-temporal pattern, and the direction this research has gone. It has been taken for granted that since patterns in space tell much about populations, then so must patterns in space and time. Although the

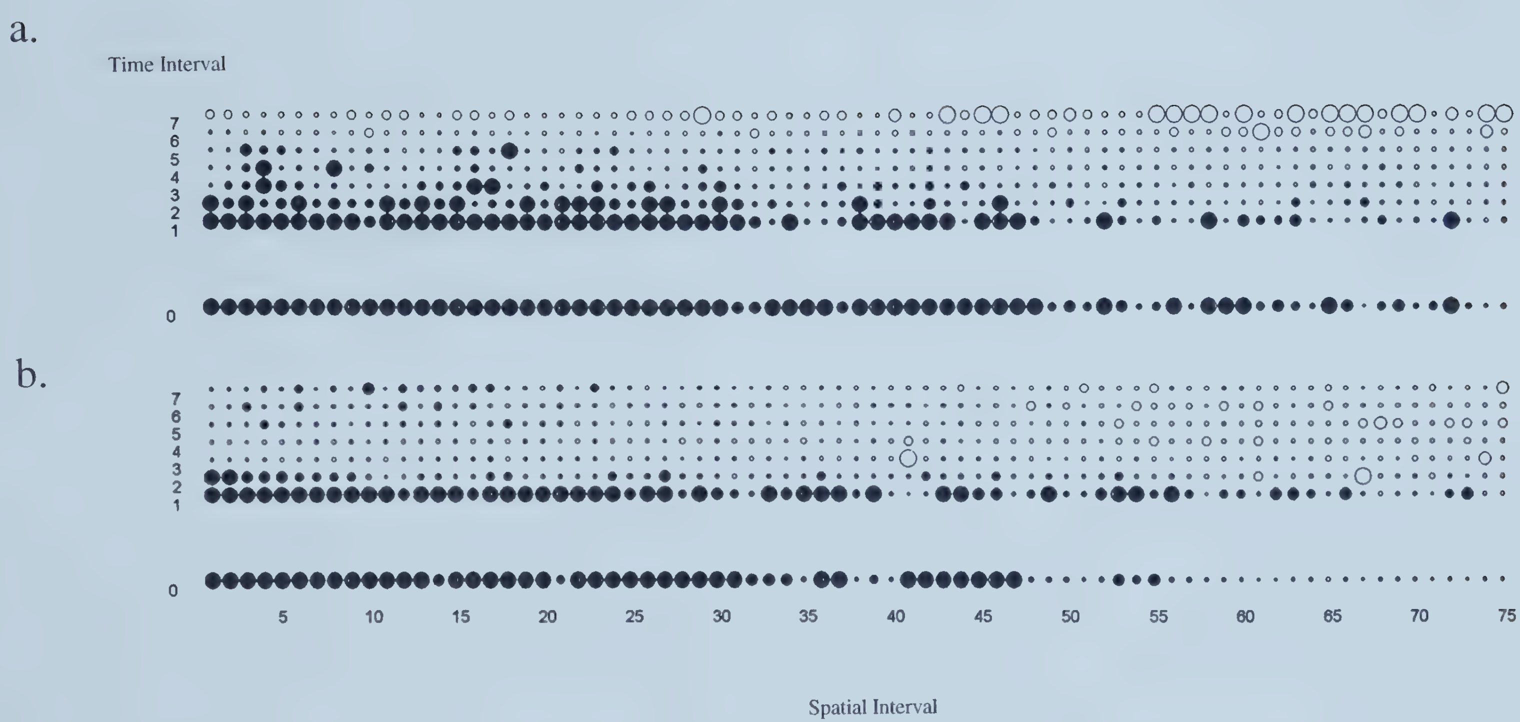

Figure 3-7. Two-factor correlograms using the Full Randomized Cell model for join count statistics on data from a. transect 1, and b. transect 2 of the Wandering River site. Filled/open circles depict where more/less joins occurred in that particular join class than were expected from randomness. Circle size indicates statistical significance, (largest $P < 0.01$).

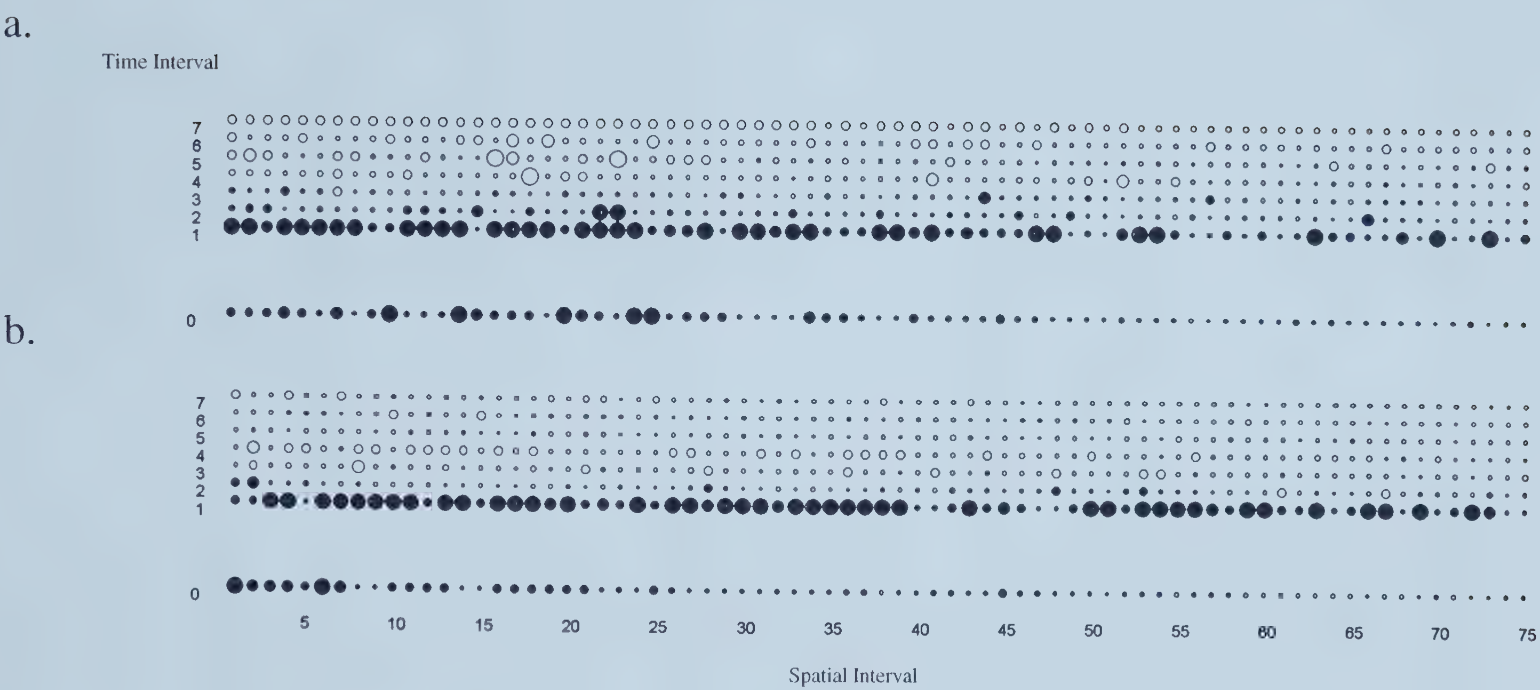

Figure 3-8. Two-factor correlograms using the Uniform Row model for join count statistics on data from a. transect 1, and b. transect 2 of the Wandering River site. Filled/open circles depict where more/less joins occurred in that particular join class than were expected from randomness. Circle size indicates statistical significance, (largest $P < 0.01$).

spatio-temporal pattern found in a clone creeping into a grassland is insightful, it is simple and probably unlikely in more complicated communities. What then, could it mean for different ages of stems to be spatially aggregated, or segregated in such communities? In the next chapter, I suggest that it has the potential to indicate whether establishment is limited by dispersal ability, or by some other factor.

In the chapter that follows, instead of examining stem establishment *per se*, I focus on what happens after initial establishment, namely on intra- and interspecific competition among initial establishers. To do this, instead of examining bivariate spatial association between two age classes of stems, bivariate spatial relations are examined between two sizes of stem in a single age class.

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CHAPTER FOUR

ESTABLISHMENT PATTERNS AT DIFFERENT TIMES SINCE DISTURBANCE IN RELATION TO DISPERSAL AND SHADE TOLERANCE STRATEGIES OF BOREAL FOREST TREE SPECIES

Introduction

Fire is the primary large-scale, natural disturbance in the boreal forest, where it acts to clear most standing vegetation, and re-start forest regeneration. Recovery of post-fire boreal forest is thought to be dominated by initial floristics (Heinselman 1981, Bergeron and Dubuc 1989). This type of vegetation development, described by Egler (1954), occurs when the first plants to establish maintain their presence in an area until conditions inhibit their growth and reproduction. The first trees to establish, therefore, have a great influence on the composition of future forest.

Tree stem establishment depends on two general factors, the spatial arrangement of pre-fire vegetation, which influences where the post-fire propagules occur, and environmental conditions. One of the most important environmental factors is the gap environment (Whitmore 1989). As a post-fire forest develops, this environment becomes more dense (Weiner and Thomas 1986, Kenkel 1988) as the large open gaps created by fire are filled. In species that rely on open areas e.g. gaps, plant establishment will respond. The major goal of this study was to examine the association between species and the

establishment patterns they create in response to the changing post-fire environment. In particular, the spatial arrangement of stems of different ages will indicate how establishment has changed through time. Because the first stems to establish probably have greater influence than any other class of stems, the spatial relationship between an age group of stems and the initial establishers of that species will indicate species' establishment response to the conditions at the time of establishment.

Different species establish in different ways, but in general, there are at least two species' characteristics important to plant establishment, dispersal and survival (Houle 1995, Noble and Slayter 1980). By classifying species' dispersal ability according to reproduction strategy, Rowe (1983) ranked dispersal as the foremost criterion of species' regeneration ability. For example, *Populus tremuloides* disperses mainly by clonal ramets, but *Pinus banksiana* and *Picea glauca* disperse only by seed. These strategies create a trade-off between the rate and spatial pattern of establishment. Clonal establishment is fast, almost certain in the vicinity of the clonal root system, but unlikely at greater distances from it. Seedling establishment, however, which may be slower, is less spatially restricted.

The second characteristic, survival, has many facets, but one of the more important ones is tolerance to shade (Rowe 1983, Bergeron and Dubuc 1989, Canham 1989). Like the dispersal strategies, shade intolerant and tolerant strategies also represent a major trade-off between the rate of establishment and its spatial distribution. For example, species that are intolerant to shade are known to establish quickly, but are generally restricted to open areas. Shade tolerant species, however, are known to establish and grow more slowly, and are less spatially restricted, being able to live for long periods beneath a canopy (Whitmore 1989).

The implication of these trade-offs is that dispersal and survival strategies can be identified by establishment pattern. For example, the spatially limited dispersal ability of clones means that in order to estalbish a new area ramets must first establish beside a future occupied area. The establishment pattern for this might show a creeping habit, indicated by younger age classes being found at increasing distances from the initial colonizers. On the other hand, shade-intolerant stems are spatially limited to open areas, and their establishment pattern would show plants of similar ages clustered among themselves in gaps, but segregated from patches of the oldest, initial establishers.

In a given area, a species will display one of four combinations of dispersal and survival strategy: 1. clonal, shade-intolerant, 2. clonal, shade-tolerant, 3. seed, shade-intolerant, or 4. seed, shade-tolerant. In this study, establishment patterns of different aged stems are examined with respect to the initial establishers, for each combination of strategies. I expect the combinations involving spatially limited strategies to be associated with establishment patterns as outlined above. Of particular interest is the establishment pattern displayed by species with both the spatially limiting clonal and shade-intolerant strategies because such an examination could reveal the relative importance of each strategy.

As an alternative approach to associating species establishment strategy with pattern of establishment, I also examined the most recent establishers of a site with respect to their establishment strategy and position in a gap environment. In particular, I also hypothesized that the shade-intolerant species should be positively associated with gaps, and that this is more likely for seed dispersed species because they are less spatially restricted than clonal species.

The species chosen for each strategy combination include: *Picea mariana* (clonal, shade-tolerant), *Populus tremuloides* and *Populus balsamifera* (clonal, shade-intolerant), *Picea mariana* and *Picea glauca* (seed dispersed, shade-tolerant), and *Pinus banksiana* (seed dispersed, shade-intolerant). Clonal and seed regenerating *P. mariana* are prevalent at different latitudes, and can often be discerned by layered attachment to another tree stem. A comparison of the two strategies in the same species, I believe gives insight into establishment patterns in different environments.

Methods

Data collection

Three data sets were used to obtain one instance of each strategy combination. The area examined was situated within a relatively large (>1000 km^2) 21 year old post-fire site in central Alberta, near the Pelican Hills (55°,30' N, 113°,50' W). The soil profile consisted of relatively thin humic horizon (≤10 cm) on a gravelly sandy-silt inorganic substrate (personal observation). The canopy consisted of *P. tremuloides* and *P. banksiana*. *P. mariana* was also present below 1 m in height. In 0.25 m^2 quadrats *P. mariana*, which appeared to be growing from seed and so assumed to be seed dispersed (shade-tolerant), and *P. banksiana* (seed dispersed, shade-intolerant) stems were mapped over a 30 m x 40 m area. This area was expanded to 40 m x 40 m for *P. tremuloides* (clonal, shade-intolerant), because there were generally fewer aspen stems than the other species. From a general survey, the tree species composition surrounding this enlarged area was similar the one examined. After mapping, stems were either cut or cored as close to the ground as possible, for determining stem age

in the laboratory.

To determine the age of a stem, the cross section was sanded with 60 then 120 grit sand paper on a belt sander. Hand sanding was done with 150-220 grit sand paper, and ring counts were made under a dissecting microscope to assign year of establishment. Stems were placed in 3 year age classes.

The site was situated beside, and accessible from, a cleared corridor due to an underground pipeline installed within the previous two years. Because of a potential edge effect due to the clearing, I examined the spatial distribution of the youngest age class of each species at this site with wavelet analysis, using the Haar wavelet. Wavelet analysis is a method of analysing a stream of data for non-random pattern, e.g. a transect of contiguous quadrats. By using a pre-conceived form, or pattern, called the wavelet, this method can reveal certain structure at different positions along a data stream, and at different scales (Dale and Mah 1998). Because of its shape, the Haar wavelet (Figure 4-1) is particularly appropriate for determining edges in pattern (Bradshaw and Spies 1992). There are two orientations to it: 1. a block of quadrats of low abundance followed by a block of high abundance quadrats (low-to-high orientation), or 2. a block of high abundance followed by a block of low abundance (high-to-low orientation). For the analysis I used the former (Figure 4-1a).

Wavelet analysis was performed on each of the 0.5 m wide, 40 m long, adjacent transects that extended perpendicular to the edge. Wavelet transform values of each quadrat

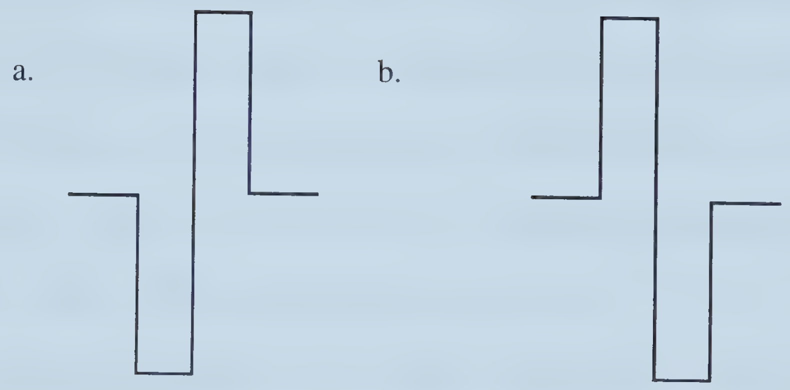


Figure 4-1. Two orientations of the Haar wavelet. Wavelet **a.** is used in the analysis of artificial data and data from the Alberta site.

position along the transects were averaged, and reported in a single "scalogram". A scalogram represents how well a particular position along the data stream fits different sizes of the wavelet. For an added comparison the analysis was done on transects that ran parallel to the edge.

As an example of how an edge would be viewed with wavelet analysis, artificial data sets were examined. The first consisted of an 80 quadrat transect with an edge occurring at quadrat 25. The second artificial data set consisted of three 80 quadrat transects, with edges at quadrats 25, 27 and 30. Wavelet analysis of this data set, thus consisted of a mean tranform value from individual analysis of the three transects.

The other data sets used for associating establishment strategy to establishment pattern came from the published accounts of Legère and Payette (1981) and Brodie (1993). The Légèr and Payette (1981) data set contained a map of 497 stems in a 14 m x 14 m area of clonal *Picea mariana* (clonal, shade-tolerant) stand >50 years old, in northern Québec. This map was scanned into a 1000 X 1000 pixel image and each live stem was placed into a 50 X 50 pixel quadrat. Stem age classes included two shrubby layers: prostrate (0-1 m) and erect (1-2 m), which the authors found to be the youngest stems, and six arborescent layers (>2 m height, Legère and Payette 1981). Of the six arborescent age classes, I grouped the two youngest into a single class, and the two oldest classes into a single class.

The last dataset came from Brodie (1993), also shown in Brodie et al. (1995), and contained a map of 750 stems of three species, *P. balsamifera* (clonal, shade-intolerant), *P. mariana* and *P. glauca* (seed dispersed, shade-tolerant), in a 70 m x 70 m area of the forest tundra zone of subarctic Québec. A quadrat size of 1 m x 1 m with 5 year age classes was

used.

Spatial analysis between the initial establishers and different age classes of stems

The spatial pattern of stems in a single age class was analysed by comparing the observed number of stems within radius *d* of each stem, to the median obtained when the stems were randomly arranged. Bivariate spatial association between two age classes was analysed by counting all of the stems of the younger age class that were within radius *d* of each stem of the older age class. This number was compared to the median obtained when the position of the older age class stems were fixed and the younger stems were randomly arranged. For each analysis, 500 randomly generated arrangements gave the random or null probability distribution, along with associated median, mean and standard deviation, of neighbours within a given radius.

A positive deviation indicated clustered or aggregated stems, and negative indicated regular or segregated. The value of a deviation from the median was divided by the standard deviation of the random distribution, giving a standardized deviate. The resulting statistic indicated the difference, in standard deviation units, between the observed value and the median. The median was used as a measure of central tendency because 50% of the random generations would occur on either side. The distributions obtained from randomization procedures were often skewed, and so the mean did not share this property. Using the median thus made determining statistical significance easier because *P*-values were obtained from the percentile that the observed number of stems occupied away from the median. Results were plotted as a function of distance *d*.

Using stem counts within a given radius of each stem is a similar approach to other well known methods such as Ripley's K function for point pattern analysis, and autocorrelation analysis (cf. Cressie 1991). Two of the characteristics that set this technique apart from K function analysis is that the data came from a grid of quadrats instead of a point pattern, and that the observed counts were not divided by the observed intensity (cf. Diggle 1983). Neither should make a difference, however, because expected values were not obtained from a hypothetical probability distribution, but from a randomization procedure. The analysis had two further benefits: first, an edge correction factor was not needed because it was based on a randomization procedure, and second, by counting the number of one type of stem within a certain distance of another, it was an easy extension to examine the bivariate association between plants of different types. Furthermore, as the bivariate version of Ripley's K function is symmetric, this approach is also.

Association between the most recent establishers and the gap environment

The second approach of this study, which tested the association between the gap environment and the most recently establishing stems, only examined the data of the Alberta site. Therefore, only three of the four establishment strategy combinations were examined for their association with gaps or non-gaps. The gap environment was quantified by the distribution of "large", "canopy" trees, irrespective of species. These were trees that were >5 cm diameter at ground height (dgh). This size class was arbitrarily decided after the ages of all stems were determined. It was, therefore, used to estimate the gap environment after the site was sampled. After determining the spatial position of all "large" stems in the 30 m X

40 m site, all quadrats were then assigned a value determined from the distance, in quadrats, to the nearest "large" tree. Thus, quadrats that were far from "large" trees relative to other quadrats were considered as being in gaps. Because the edge of the site would not accurately indicate whether quadrats were close to a "large" stem, a buffer of three quadrats was placed around the site and only quadrats within this area were examined.

After characterizing the gap environment by assigning each quadrat a value according to its distance to the nearest "large" tree, the association between species, establishment strategy and gap environment was analysed as a contingency table. This 6 x 3 table showed the number of stems of a particular strategy that were found at a particular distance from the "large" stems. It was compared to a table derived from a null hypothesis that there was no association between establishment strategy and distance to nearest "large" tree.

The overall approach was based on a simple case of the "fourth-corner problem" described by Legendre et al. (1997). A "fourth-corner problem" uses three related data matrices to obtain a fourth. In particular, a species by site matrix, **A**, an environmental variable by site matrix, **C**, and a species by biological traits matrix, **B**, are all used to estimate a fourth matrix **D** of environmental by biological traits (Figure 4-2). Using this method, biological or behavioral traits can be linked to environmental characteristics (Legendre et al. 1997). I used this method to determine whether certain combinations of dispersal and survival strategies are association at certain distances from "large" trees.

Although the usual method of statistically testing a contingency table is by using the

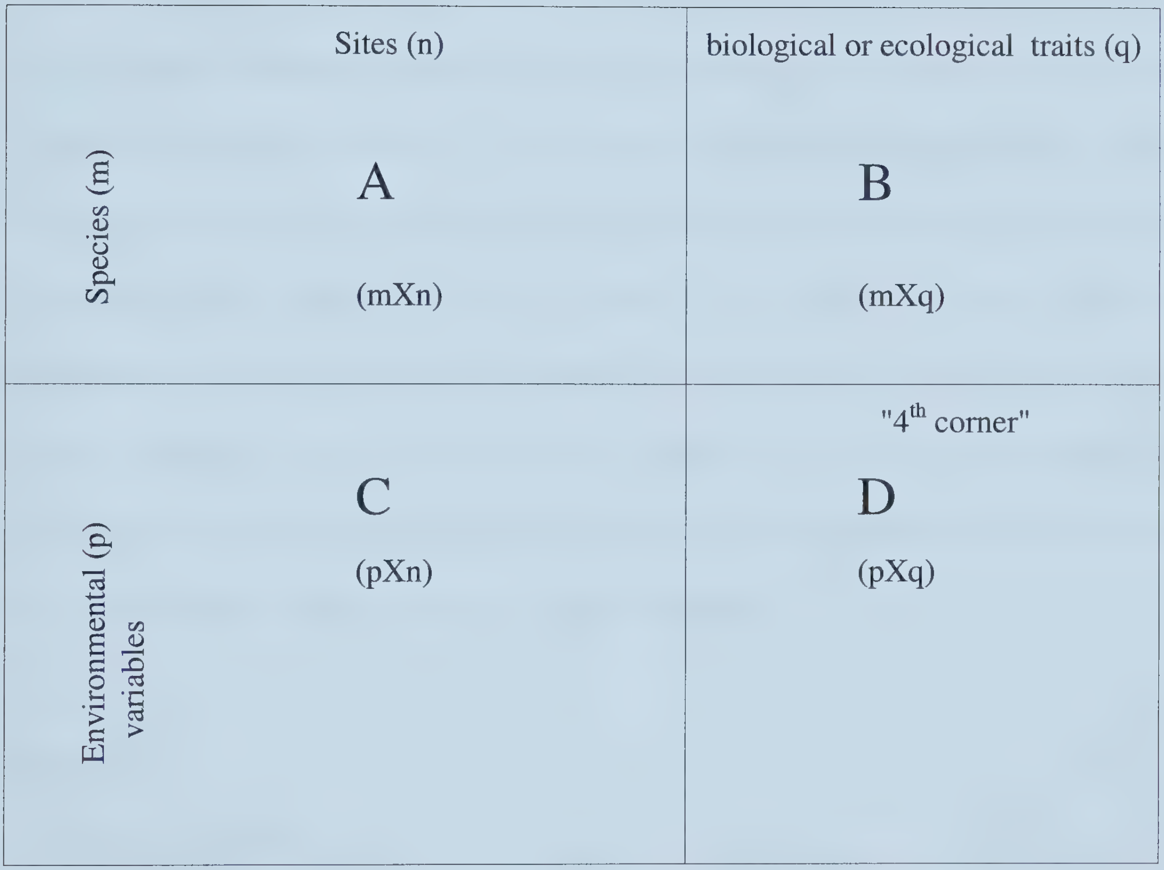


Figure 4-2. Illustration of the fourth corner problem (Legendre et al. 1997). Data matrices **A**, **B**, and **C** are used to determine matrix **D**, the association between biological-ecological characteristics and environmental variables.

G or Pearson's X^2 statistic, Legendre et al. (1997) suggest using a randomization procedure because observations are often not independent. There are many types of randomization procedures, which test different null hypotheses, but in this case, a null hypothesis of random species association within the environment is tested. The randomization procedure for this null hypothesis consisted of randomly, and independently, re-arranging the rows of the species by site matrix. After each of 1000 realizations of the randomization procedure, matrix **D**, giving the frequency of each strategy at each distance from the "large" stems, was re-calculated, and a *G* statistic derived (Zar 1996). For the 1000 realizations of the null hypothesis, a frequency or probability distribution was obtained for the *G* statistic of the entire contingency table, and for each cell in matrix **D**. A one-sided statistical test was performed on the *G* statistic and cell entries, and a *P*-value obtained based on the percentile the observed value took from the mean of the distribution.

Results

Age class distributions

The spatial arrangement of species' age classes are almost all aggregated (Table 4-1). Age class distributions of the seed regenerating species were all unimodal. These included: *P. banksiana* and *P. mariana* at the Alberta site (Figure 4-3), and the combined *Picea* spp. of Brodie (1993). Of the clonal species, Brodie (1993) found a reverse-J age class distribution in *P. balsamifera*, but the *P. tremuloides* at the Pelican Hills site showed more of a J-shaped

Table 4-1. Results of spatial pattern analysis of stems classified by age class, species and data set. + indicates stems were clustered, o indicates no pattern was apparent i.e. not different from complete spatial randomness.

Site / data set	Species	Age Class		Site / data set	Species	Age Class	
Alberta	*P. tremuloides*	1	+	Quebec	*P. balsamifera*	0-19	+
		2	+		(analysis results from Brodie et al. 1995)	20-39 years	o
		3	o			40-54 years	+
		4	o				
		5	+				
		6	+				
		7	+		*Picea* spp.	1+2	+
						3	+
						4	+
	P. banksiana	1+2	+			5	+
		3	+			6	+
		4	+			7+8	+
		5	+				
		6	+				
		7	+	Leger and Payette	*P. mariana*	1 (prostrate)	+
						2 (erect)	+
	P. mariana	1+2	+			3	+
		3	+			4	+
		4	+			5	+
		5	+			6+7	+
		6	+				
		7	+				

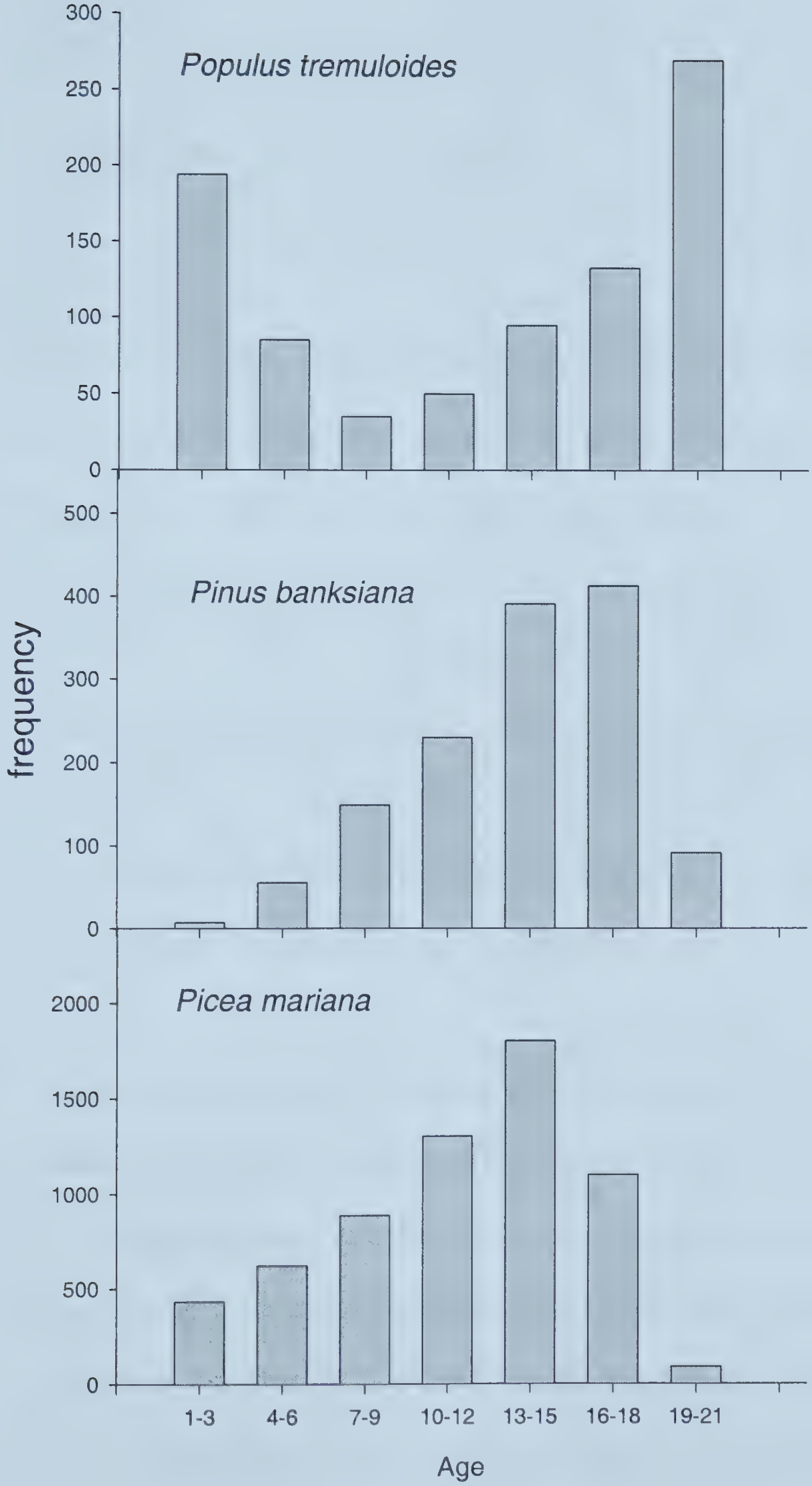


Figure 4-3. Age class frequency distribution of the three tree species at Alberta site.

age class distribution (Figure 4-3). Légèr and Payette (1981) found a monotonically decreasing age class distribution for clonal *P. mariana*.

Wavelet analysis

Figure 4-4 shows the wavelet analysis of the single artificial transect (Figure 4-4a), the mean wavelet transform (Figure 4-4b) of the three transects, and the actual artifical data used (Figure 4-4c). The figure shows an inverse or negative fit, at all block sizes or scales, of the wavelet used (Figure 4-1a) at quadrat 25 of the transect. This indicates that the orientation of the edge is opposite to that of Figure 4-1a, which is confirmed in Figure 4-1c. The mean transform of the three transects (Figure 4-4b) also corresponds to edges in the artificial data.

Because there were so few *P. banksiana* stems of age class 1, edge detection with wavelet analysis was not done on this species. No edge appeared in the *P. mariana* (Figure 4-5), but one is apparent for *P. tremuloides* in the first 2 m of the transect.

Spatial patterns of age classes and spatial association between age classes

Spatial association between age classes in the clonal black spruce (Figure 4-6), shows that bands of decreasing age classes are generally found at increasing distance from the oldest stems. For example, age class 5 stems are significantly aggregated around the oldest age class, 6, at a range from 1 to 7 quadrats (0.25 m^2). Age classes 4 and 3 are each aggregated about the oldest stems at a range from 3 to 9, and from 2 to 8, respectively. The youngest age

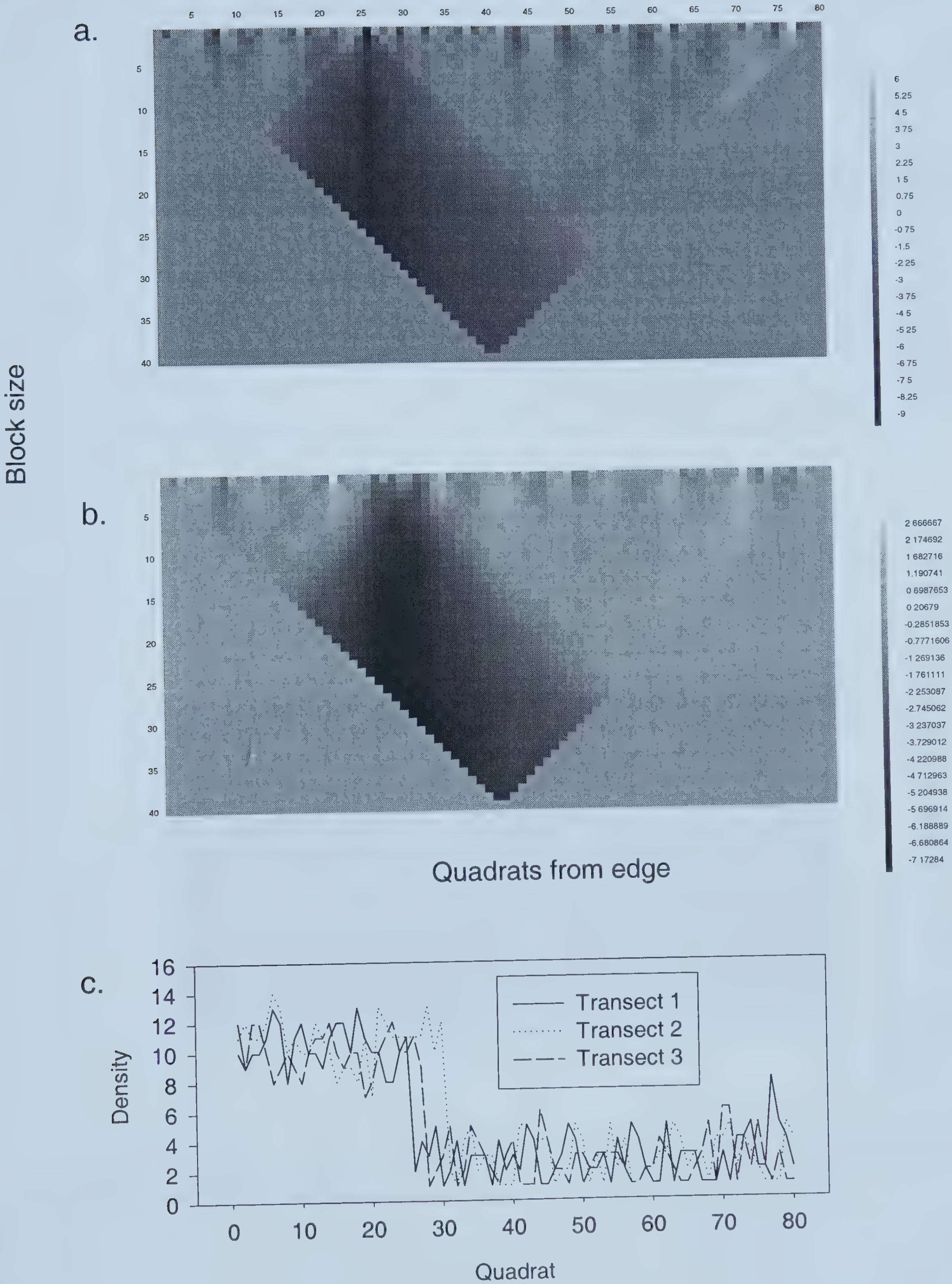
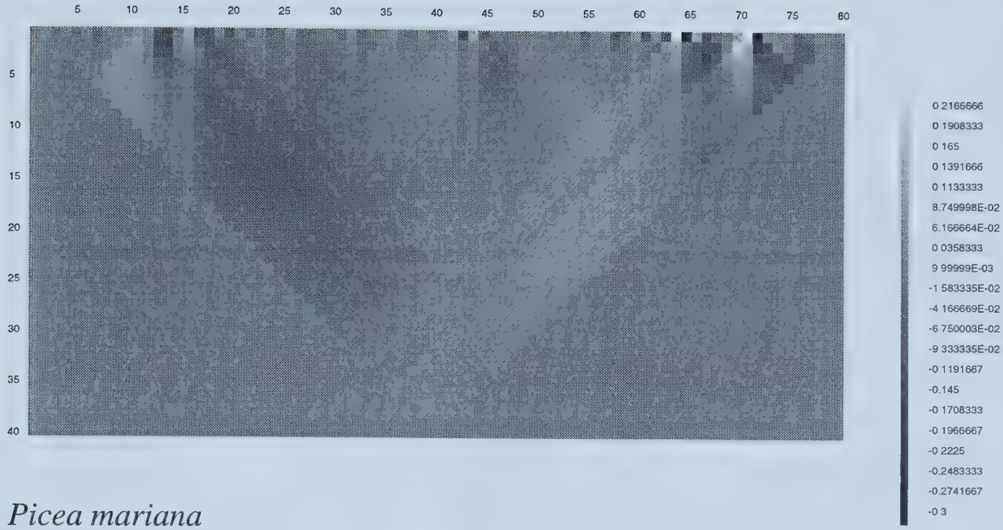


Figure 4-4. Wavelet scalogram of a. artifical transect 1, b. mean of the three artificial transects, and c. actual values along the artificial transects.



Picea mariana

Populus tremuloides

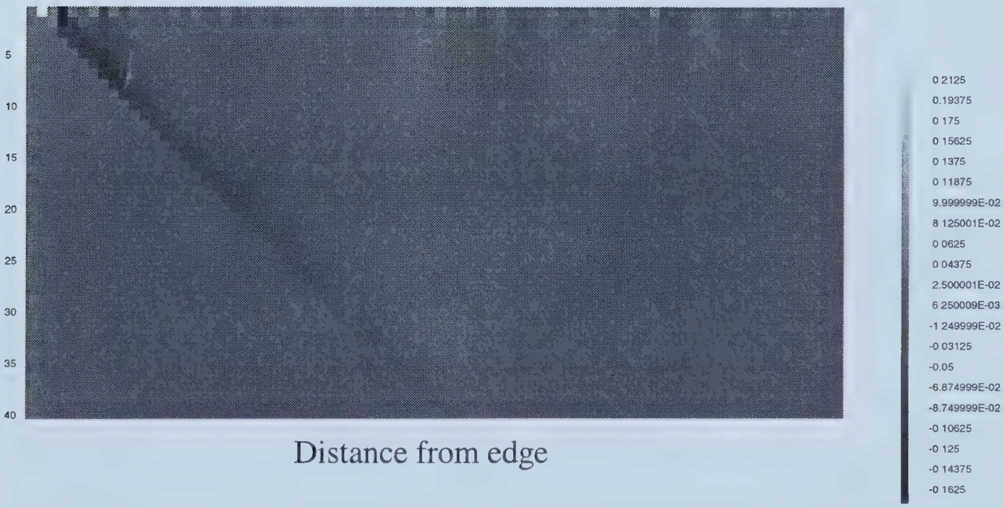


Figure 4-5. Mean wavelet scalogram across contiguous transects in Alberta site for *P. tremuloides* and *P. mariana*.

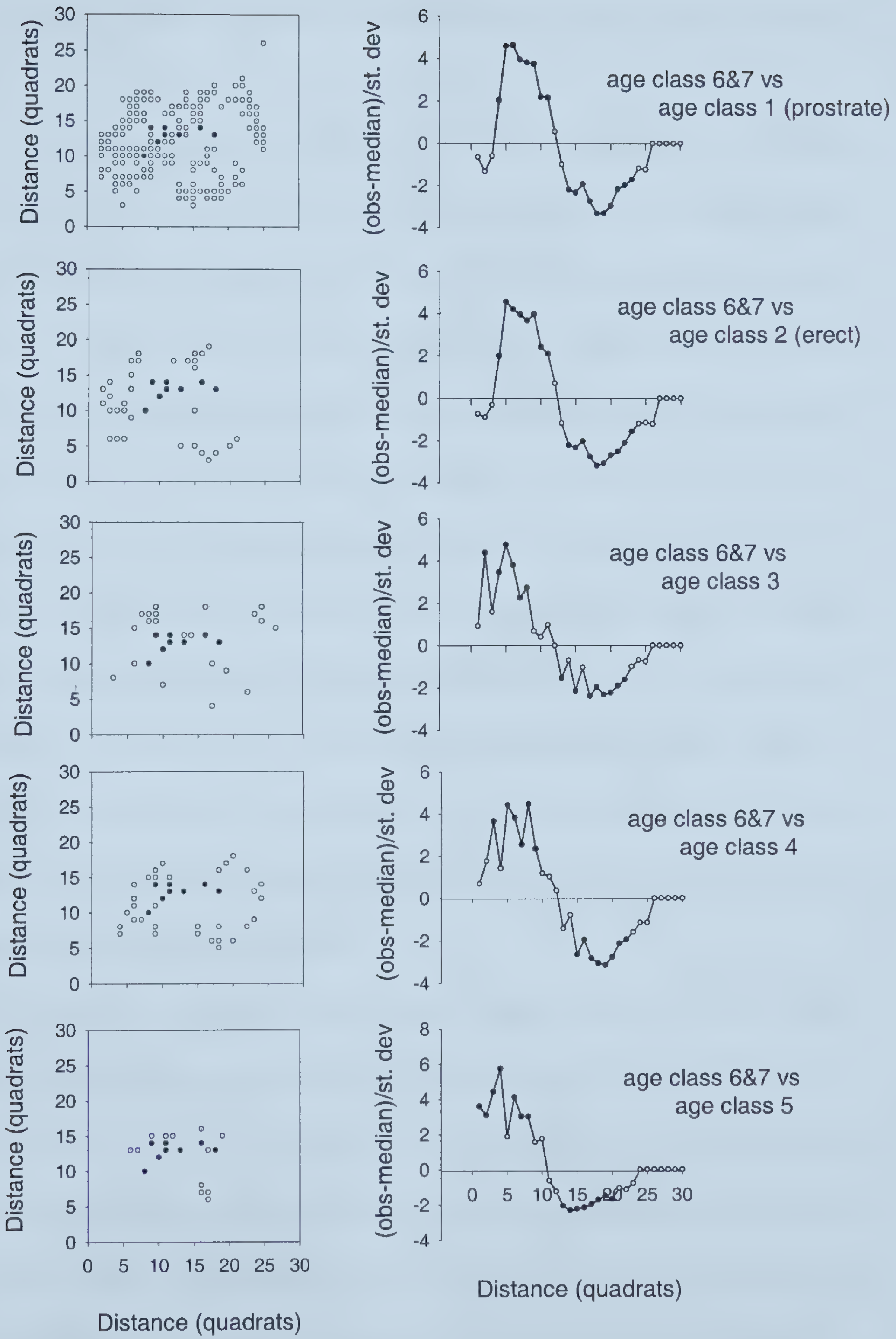


Figure 4-6. Spatial distribution and bivariate analysis between the oldest age class of stems and each of the younger age classes for clonal, shade-tolerant *P. mariana* of Leger and Payette (1981). Filled circles in the arrangements on the left indicate the oldest initial establishers, filled circles in the correlograms on the right indicate statistical significance $P < 0.05$ (one-sided test).

classes i.e. the two shrubby forms, were found aggregated at even farther distances of between 4 and 11.

The results from the data set of Brodie (1993) for *P. balsamifera* show that, in general, the youngest stems, age class 1, were mainly found aggregated at distances greater than 50 quadrats from the initial establishers (Figure 4-7). Older age classes were found closer at between 25 and 30 quadrats, and the oldest age classes tended to be more closely associated with the initial establishers, generally within a distance of about 20 quadrats. Such a pattern did not occur in the seed generated spruce (Figure 4-8a and b) whose stems were generally aggregated about the initial establishers, irrespective of age class.

Establishment patterns in the Alberta site showed that the most recently established pine seedlings were segregated from the oldest trees (Figure 4-9). However, a single patch of trees in the lower left corner of the site plot (Figure 4-9) probably has great influence on these results. With increasing time, i.e. decreasing age class, new stems went from being highly clustered at close distances, through a period of more random establishment, to being highly segregated from the initial establishers.

In the *P. tremuloides*, the reason for detecting an edge in the wavelet analysis can be seen in the high concentration of young stems in the top left part of the area (Figure 4-10). Whether this was due to being next to the pipeline on the left part of the stem plot of the figure, cannot be determined with certainty. However, in the next oldest age class (stems 4-6 years) there is again a high concentration of stems on the left side of the area (Figure 4-10) which may indicate that increased establishment was high in this area before the pipeline was installed.

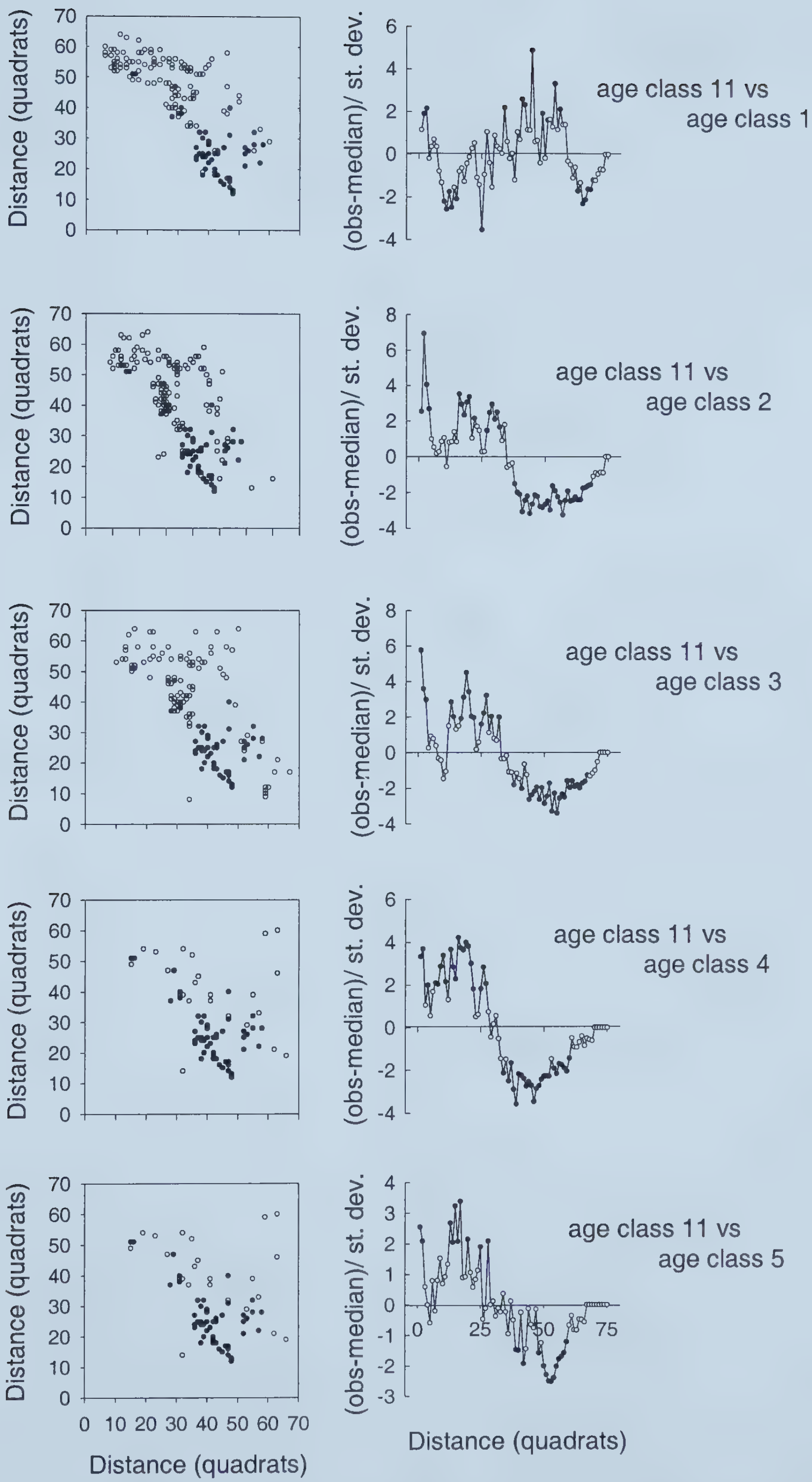


Figure 4-7a. Spatial distribution and bivariate analysis between the oldest aged stems and each of the five youngest age classes of clonal, shade-intolerant *P. balsamifera* stems in the Quebec dataset. Filled circles in the spatial arrangements on the left indicate the initial establishers, filled circles on the correlograms on the right indicate statistical significance $P < 0.05$ (one-sided test).

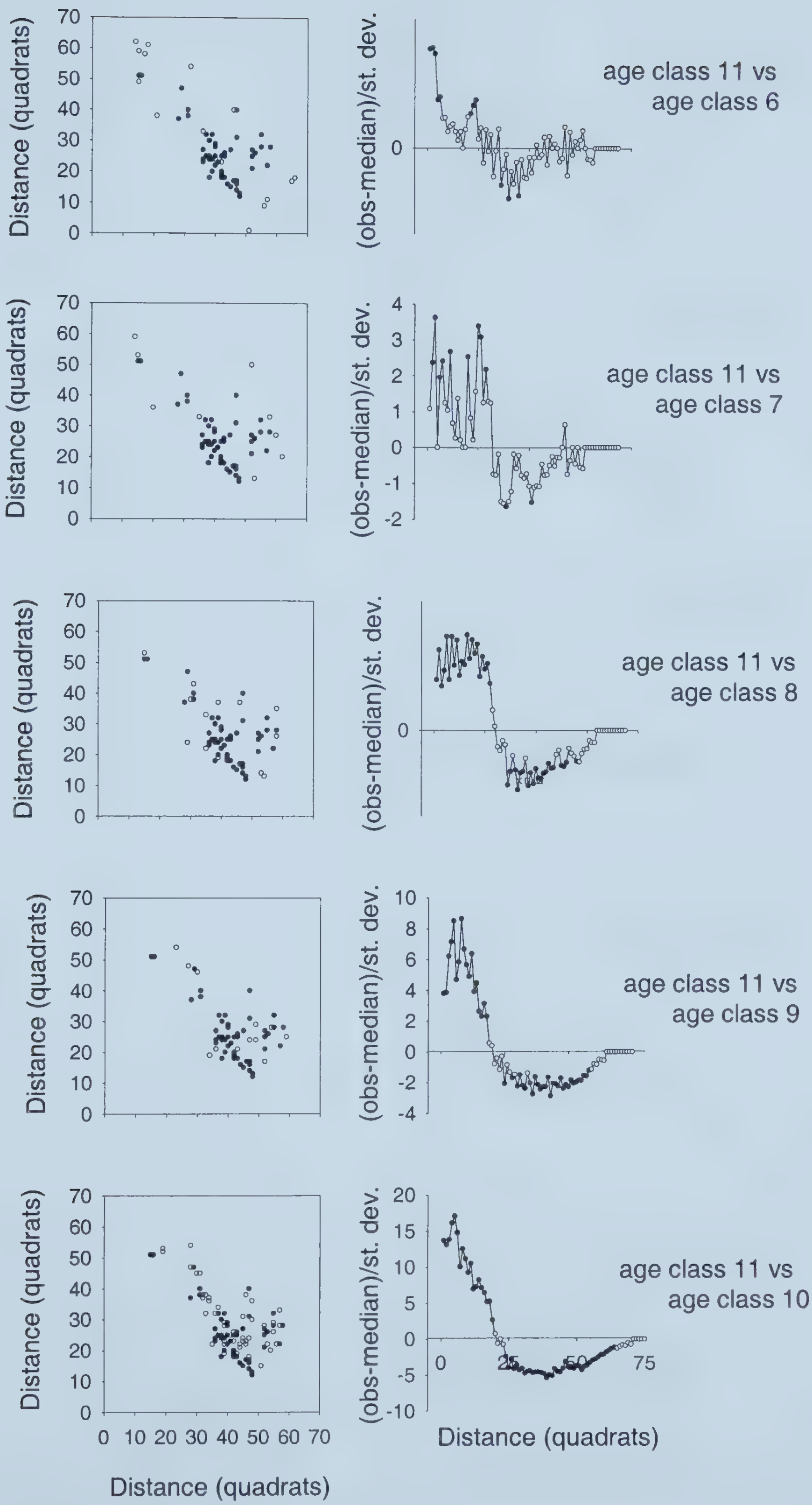


Figure 4-7b. Spatial distribution and bivariate analysis between the oldest aged stems and each of the other five oldest classes of clonal shade-intolerant *P. balsamifera* stems for the Quebec dataset. Filled circles in the spatial arrangements on the left indicate the initial establishers, filled circles on the correlograms on the right indicate statistical significance $P<0.05$ (one-sided test).

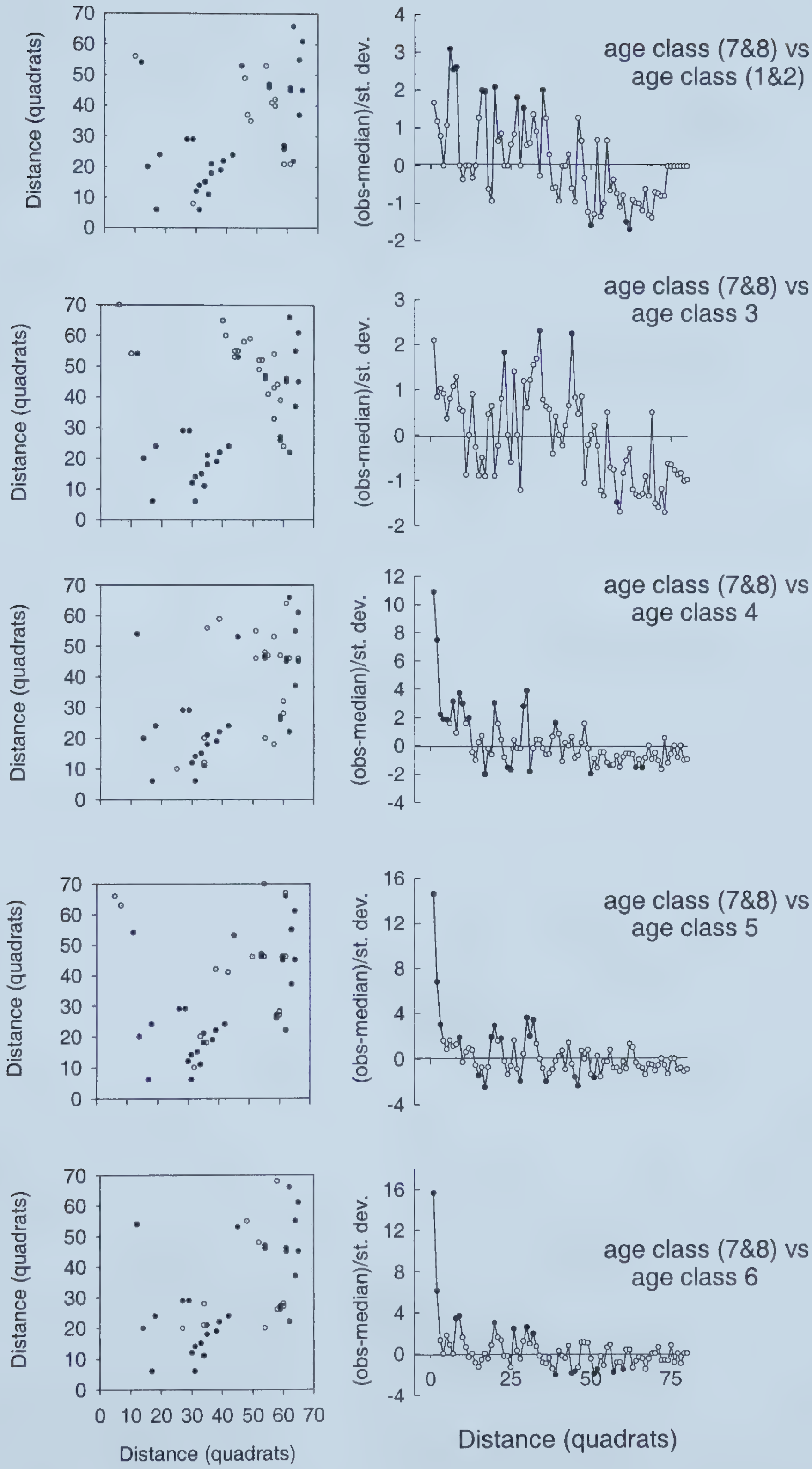


Figure 4-8a. Spatial distribution and bivariate analysis between the oldest stems and each younger age class of seed dispersed, shade-tolerant *P. mariana* stems in the Quebec dataset. Filled circles in the spatial arrangements on the left indicate the intial establishers, filled circles in the correlograms on the right indicate statistical significance $P < 0.05$ (one-sided test).

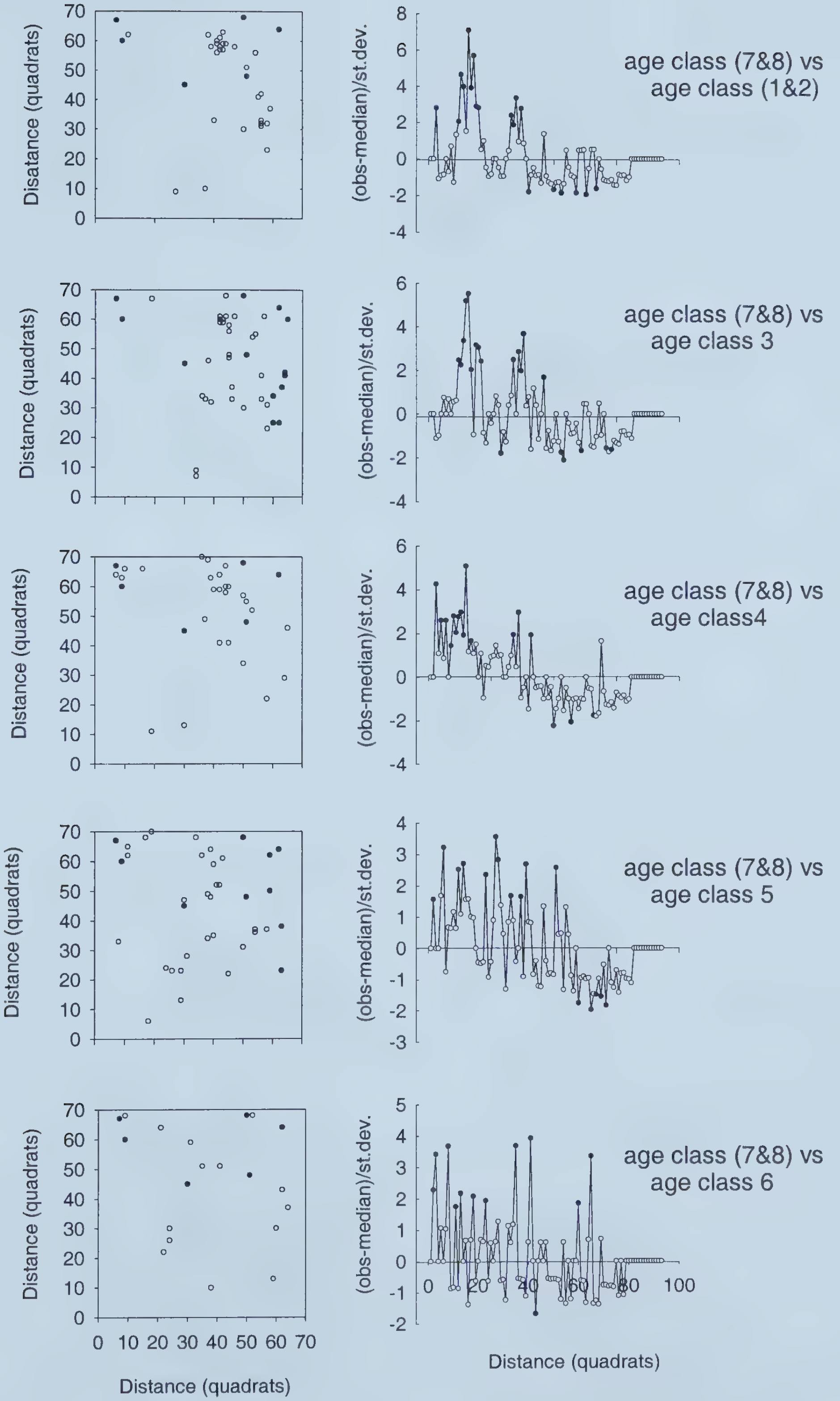


Figure 4-8b. Spatial distribution and bivariate analysis between the oldest stems and each younger age class of seed dispersed, shade tolerant *P. glauca* stems in the Quebec dataset. Filled circles in the spatial arrangements on the left indicate the initial establishers, filled circles in the correlograms on the right indicate statistical significance *P* <0.05 (one-sided test).

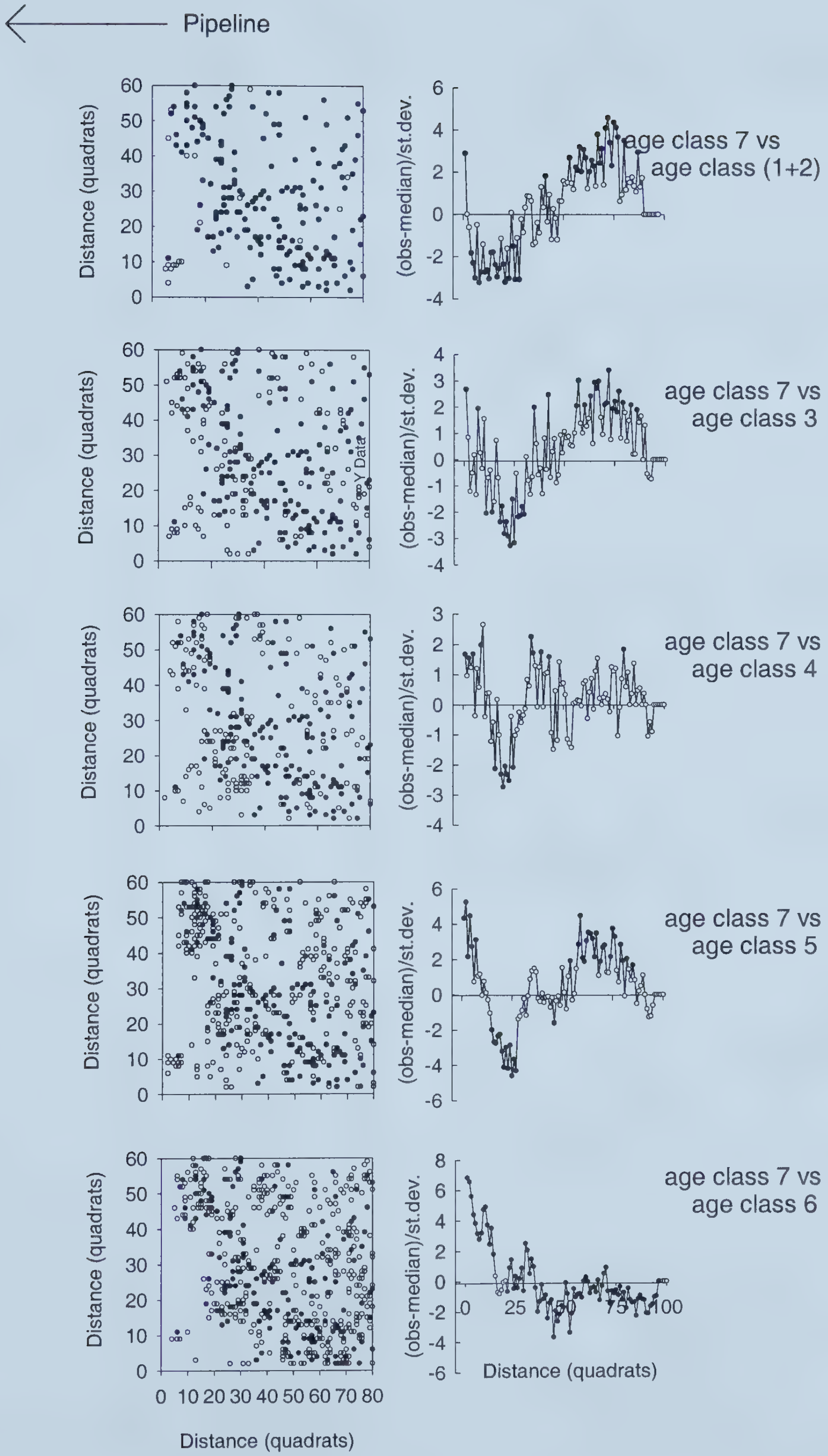


Figure 4-9. Spatial arrangment and bivariate spatial association between the oldest age class of stems and each of the five younger age classes of seed dispersed, shade-tolerant *P. banksiana* in the Alberta site. Filled circles in the arrangements on the left indicate the initial establishers, filled circles on the correlograms on the right indicate statistical significance $P < 0.05$ (one-sided test).

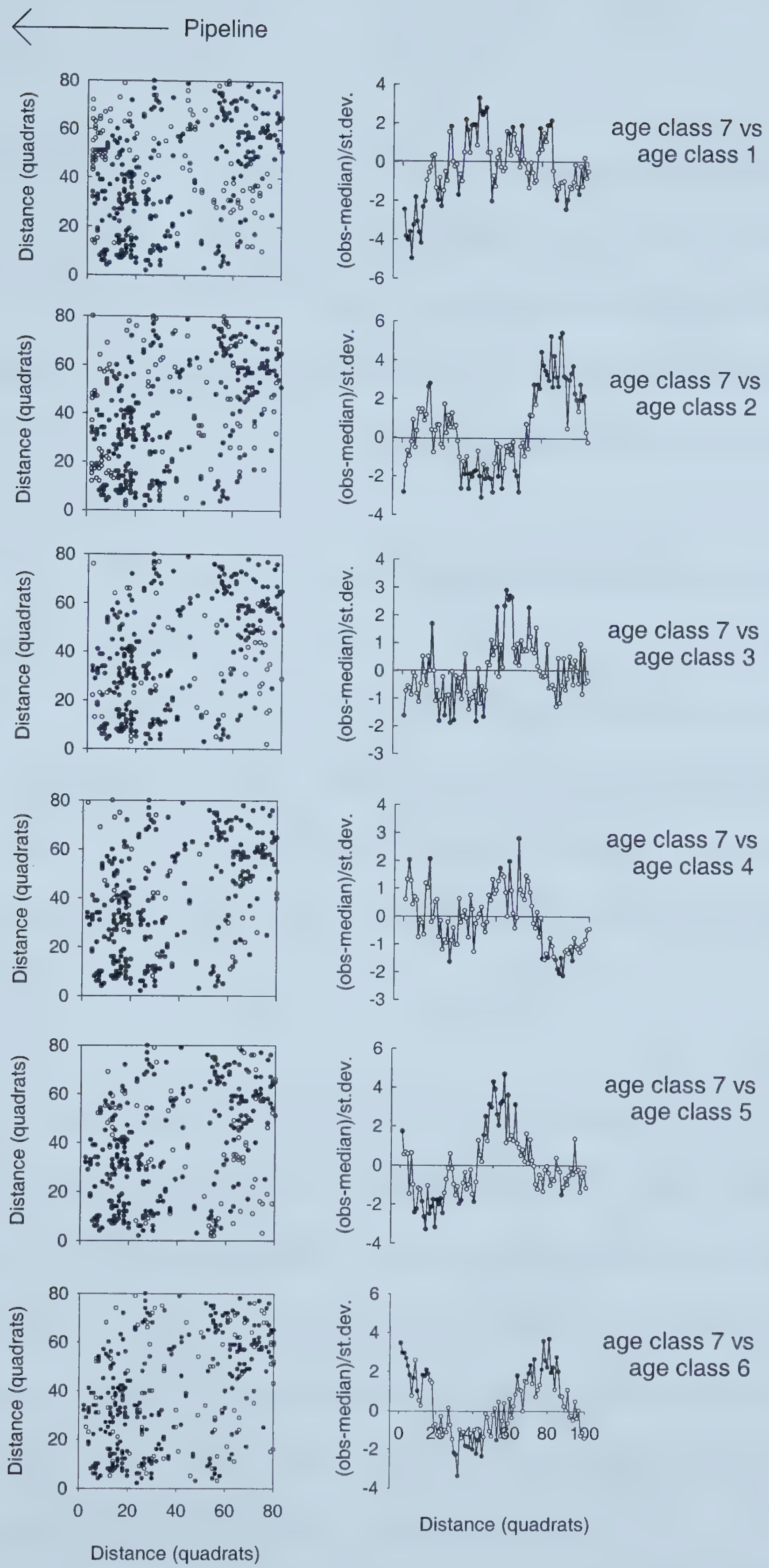


Figure 4-10. Spatial arrangement and bivariate spatial association between the oldest age class of stems and each of the six younger age classes of clonal, shade-intolerant *P. tremuloides* in the Alberta site. Filled circles in the arrangements on the left indicate the initial establishers, filled circles in the correlograms on the right indicate statistical significance $P < 0.05$ (one-sided test).

Two patches of early *P. tremuloides* establishers are evident. The correlogram showing the spatial association between age class 6 and age class 7, the two oldest age classes, in Figure 4-10 illustrates this: two high density regions separated by a very low density, sparsely populated, region. Younger age classes, especially age class 1, fill this area with no particular pattern, until the most recent establishers were found strongly clustered in the area between the patches.

Establishment patterns for the *P. mariana* shows all age classes strongly aggregated around the oldest stems (Figure 4-11). Similar to the aspen, early colonizers showed a relatively large-scale patchy pattern, perhaps reflecting the pre-fire distribution of black spruce. Unlike aspen, however, the spatial relation between age classes did not change substantially with time. All age classes appeared to have the same spatial relation to the initial colonizers, and the large magnitude of the autocorrelation values reflect the great number of stems in the site.

Association between the most recent establishers and the gap environment

The gap environment, characterized by the distance of each quadrat to the nearest "large" tree is shown in Figure 4-12. The most open gaps, i.e. those that were the farthest from a "large" stem, were at the edges of the area. This is almost certainly an edge effect. Except for these, the number of quadrats at different distances is about the same in the interior portion as the entire area (Figure 4-13). The test using the G statistic showed no association between establishment strategy and distance from "large" trees (Table 4-2).

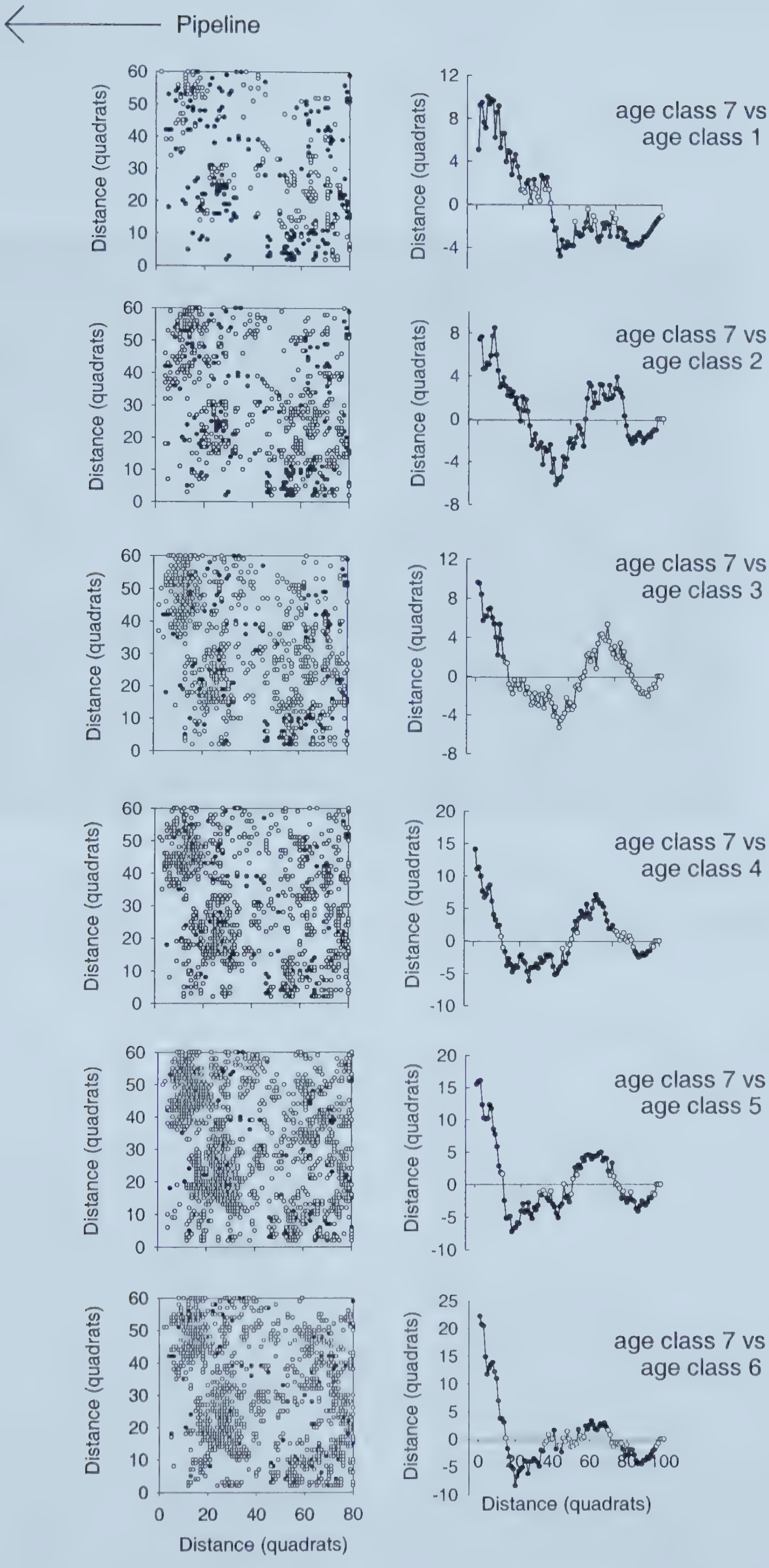


Figure 4-11. Spatial arrangement and bivariate spatial association between the oldest age class of stems and each of the six younger age classes of seed dispersed, shade-tolerant *P. mariana* in the Alberta site. Filled circles in the arrangements on the left indicate the initial establishers, filled circles in the correlograms on the right indicate statistical significance $P < 0.05$ (one-sided test).

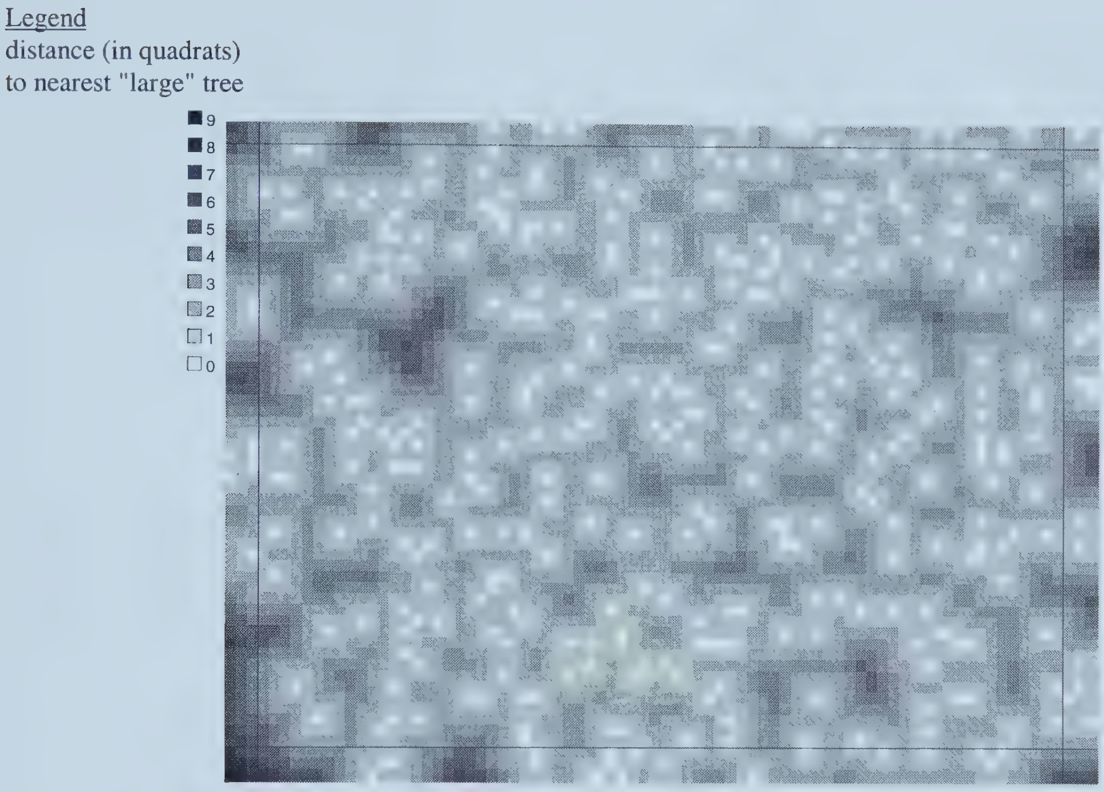


Figure 4-12. The gap environment at the Alberta site where quadrats are assigned distance to the nearest "large" tree (i.e. >5 cm dgh). Large trees consisted of *P. banksiana* and *P. tremuloides*.

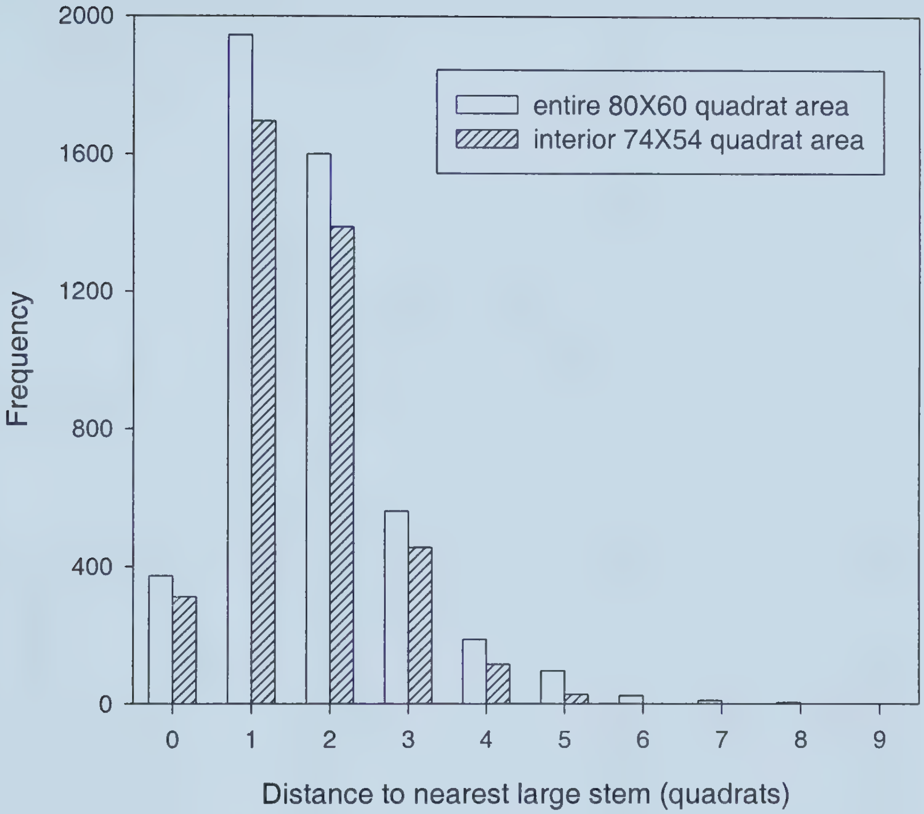


Figure 4-13. Frequency distributions of quadrats according to distance to nearest "large" tree (i.e. < 5cm dgh). Large trees consisted of *P. banksiana* and *P. tremuloides.*

Table 4-2. Association between species, dispersal and survival strategy, and the gap environment, measured as distance to nearest "large" tree. G-statistic and overall test of significance is shown at the bottom of table. Cells of the table show the number of particular stems found at different distances from large trees. A statistical test on these association was made based on H_0 that species were randomly associated with this gap environment. "+" indicates the value was greater than expected under H_0, "-" indicates it was less, and *P*-value is shown below.

		Strategy/species		
		clonal, shade-intolerant, *P. tremuloides*	seed, shade-intolerant, *P. banksiana*	seed, shade-tolerant, *P. mariana*
Distance to nearest "large" tree (quadrats)	0	4- 0.43	2+ 0.54	18+ 0.33
	1	25- 0.39	12+ 0.21	107+ 0.02
	2	24+ 0.33	4- 0.11	56- 0.03
	3	7- 0.57	3+ 0.42	17- 0.13
	4	3+ 0.27	0- 0.30	3- 0.20
	5	0- 0.25	1+ 0.09	4+ 0.10

G=5.83, *P*=0.57

Discussion

Previous studies investigating establishment patterns in post-fire boreal forest (Houle 1995, Sirois 1995) have focused on spatial relations among life history stages. This study examined spatial arrangements of tree ages, thereby concentrating on a smaller time scale. This study also went further, however, in two attempts to relate different establishment patterns to species' regeneration strategy. One attempt, the contingency table analysis, showed that in the most recently established trees of one site, no strategy was associated with a particular gap or patch environment, defined as the distance from "large" trees. A more accurate estimation of what constitutes a patch and a gap, perhaps based on light quantity or quality (cf. Endler 1993) could provide information for a more definitive result. Results from the spatial association between the oldest intitial establishers and different age classes, however, did indicate that stem establishment over time varied according to establishment strategy.

The purpose for choosing the data sets used in this study was to obtain one instance for each of the possible dispersal and survival strategy combinations. In the end, two instances of the clonal, shade-intolerant combination were examined. All data sets had a common theme: each contained spatial and age information of boreal forest tree species, detailing the spatial relationship between different age classes of stems. In the data sets that came from published sources, this was slightly different from the authors' original treatment. However, the original publications still offered important insight, and the results found here either expanded on certain aspects of the the analyses, or supported the original conclusions.

For example, results support the observation of Légèr and Payette (1981) of radial expansion of the black spruce clone. Younger stems tended to be found aggregated at

increasing distances from the oldest stems. This creeping type of growth was expected because *P. mariana* was reproducing vegetatively at this site, and so dispersal ability was limited. Such clonal expansion is known to create a "candelabrum" spruce, where a tall individual is surrounded by smaller stems (Viereck and Johnson 1990).

At the other sites, where *P. mariana* and *P. glauca* were apparently regenerating from seed (pers. obs.), establishment patterns changed little with time. In other words, most age classes were aggregated about the initial establishers at roughly the same scale. The facultative reproductive ability displayed by *P. mariana* emphasizes that different strategies operate under different environmental conditions. Asexual reproduction, in general, is more common at high latitudes (Maynard Smith 1978), and in black spruce, it is thought to be more common in open areas (Viereck and Johnson 1990), like those of Légèr and Payette (1981).

In the original treatment of her data, Brodie (1993) showed a highly clustered group of old *P. balsamifera* stems, followed by a second wave of directional ramet expansion. The treatment of those data in this examination differed by concentrating on spatial association between age classes rather than within them, but the results support the original conclusions. Only the youngest stems are segregated from the immediate neighbourhood of the initial establishers. At greater distances they were aggregated. The middle age classes tended to be aggregated around the initial establishers closer than the youngest stems but farther than the oldest two ages classes. This suggests, not gradual clonal creep as shown in the black spruce, but rather two or three surges of ramet establishment. As Brodie (1993) noted, similar growth has been shown before in discontinuous growth profiles of *P. balsamifera* by Comtois and

Payette (1987). Such punctuated expansion is different from the more continuous expansion reported by Barnes (1966). Nevertheless, the lack of older stems toward the edge of the area indicates that stem establishment of this clonal shade-intolerant species was limited mainly by the clonal, rather than the shade-intolerance strategy.

Results from the clonal shade-intolerant, *P. tremuloides* of the Alberta site were in some ways reversed, because instead of a central core of initially establishing stems, there was initially a "hole" of low stem density between two high density clusters. This could have been an area between two clones. Nevertheless, the results indicate that stems of intermediate age filled in this area only slightly, and exhibited a spatial association with the initial establishers that was similar to older age classes. Only the most recent stems appeared to have surged into the central area, in a manner similar to the punctuated establishment previously discussed. Why this apparent surge of establishment occurs is difficult to tell, but a period of time may be required for the genet to replenish its ability to support an expansion of high density suckers.

Ramet sprouting is known to be highly dependent on temperature and light (Peterson and Peterson 1992). In an open stand, like the Québec site, new establishment will occur at the fringes where the conditions and room to expand exist, and in a closed stand, new establishment will occur in canopy gaps. It is not clear, however, whether the surge in *Populus* ramets at the Alberta site occurred in entirely open gap conditions, because the area between the two aspen patches contained a high density of initial *P. banksiana* establishers which were relatively large, and shaded much of the ground (pers. obs). Therefore, a single species univariate approach may be misleading because such factors as shade quality between

aspen and pine (Ross et al. 1986) and competitive relations may explain why older aspen stems were not found in this gap. Competitive relations inferred from interspecific patterns are addressed in the next chapter.

P. banksiana initially established in the central area of the Alberta site. Although the total number of new stems decreased with time, spatial association with the initial establishers also decreased, and new stems occurred at greater distances from the initial establishers. This was different from the previous establishment patterns exhibited, namely the creeping establishment shown in clonally reproducing *P. mariana*, and the punctuated establishment displayed by the *Populus* species. In particular, it was different from the first of these because relatively old stems, such as those in age classes 4 and 5, were found to be aggregated at two scales, a small local one and a relatively larger one. This second larger scale is apparently not due to patchiness of the initial establishers, but more establishment at greater distance from the initial establishers. Establishment pattern differed from the *Populus* species because new pine establishment declined, and in such a manner that it declined more near the initial establishers, than farther away from them. The decline could be due either to local seed bank exhaustion, or to shade intolerance from a lack of sufficiently open conditions.

There are many processes that influence where and when a species is found in post-fire boreal forest. These include factors such as those in this study like the pre-fire vegetation patterns, initial floristics (Bergeron and Dubuc 1989, Stewart 1989, Davis et al. 1989), and species characteristics, like dispersal and survival ability (e.g. Thomson et al. 1996). However, there are other factors like interval between disturbances. In areas where this

interval is long, several generations of trees can occur (e.g. Galipeau et al. 1997). Under these conditions, parent-offspring relations (cf Connell 1971, McCanny 1985, Houle 1995) may occur where, for example, offspring survival depends on being far from its parent and its associated exploiters. This would result in a regular spatial arrangement of individuals in a species. Where disturbance intervals are short, trees that make it to the canopy are influenced not by parent-offspring relations, but with siblings (e.g. Willson et al. 1987) as many individuals from the same parent compete to establish and survive. Where the disturbance interval is consistently short, seed-dispersed individuals may be unable to mature enough to replenish the seed bank (Noble and Slayter 1980), and the species may vanish from the stand. Similarly for clonal species, although the spatial extent of the root system is a remnant of the former forest, and capable of surviving all but very intense burns (Brown and DeByle 1987), there is evidence (Peterson and Peterson 1992) that short disturbance intervals may eliminate it from an area if the reserves in the root system are not replenished. Although it is unlikely that disturbance intervals were this extreme in any of the sites of this study, long term climatic changes may shift the vegetation composition of the boreal forest in such a manner.

The results of this study rely on accurate stem aging. Similar to findings by Carleton (1982), stems in both the Québec and Alberta sites, generally established quickly after fire. However, it was not as sudden as that found by St.Pierre et al. (1992) who reported almost all recruitment in the first three growing seasons following fire in a *P. banksiana* and *P. mariana* forest in Québec. Aging errors were possible, particularly if errors were biased when aging small, suppressed, stems. This should be considered when interpreting the results.

In conclusion, species' regeneration strategies were seen in establishment patterns.

In particular, the clonal shade-intolerant strategy of *Populus* species in two cases showed punctuated expansion, as has been documented previously. It is commonly thought that ecological processes create observable patterns (Watt 1947). A further step in this chain in this chain of logic, however, is that different inherited species characteristics are associated with different processes, which in turn create patterns. This was appreciated by Legendre et al. (1997) in their formulation, and solution of the "fourth-corner problem". Although this particular approach failed to show a link here, there was other evidence that certain dispersal and survival strategies in the regeneration process create their own establishment patterns.

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CHAPTER FIVE

UNEXPECTED SPATIAL PATTERNS OF TREE SPECIES IN MULTI-SPECIES FORESTS

Introduction

In theory, plant competition, which includes any interaction that reduces the fitness of its participants (Crawley 1986) should produce patterns of regularly spaced individuals (Greig-Smith 1957, Pielou 1962). Although relatively few accounts of regular spatial patterns exist (Kenkel 1988), many studies (e.g. Hutchings 1978, 1979, Kenkel 1988, He et al. 1997, Martens et al. 1997) have documented a shift to greater regularity with time, such as from an initially clumped spatial pattern to a random one (Antonovics and Levin 1980). Such results illustrate that one explanation for the lack of reported regular pattern is that competition is only one of many processes that create and change the spatial arrangement of individuals (Sterner et al. 1986). In other words, competition operates on an initial spatial pattern that arise from processes like dispersal and establishment.

To infer past competition from present spatial pattern, therefore, requires knowledge of the initial spatial arrangement of individuals. Sterner et al. (1986) and Kenkel (1988) both detected intraspecific competition by observing that spatial patterns of adult stems were more regular than those obtained when stems of the initial pattern were subjected to random mortality, and when competition is investigated in this manner, there are two critical factors

to consider. First, without long-term monitoring of a population, the actual initial pattern of stems is impossible to assess, and so must be estimated in some way. Sterner et al. (1986), for example, took the approach of assuming the current spatial pattern of seedlings is basically the same pattern from which the current adults emerged. Alternatively, Kenkel (1988) used the combined spatial arrangements of living and dead *Pinus banksiana* stems, as a good estimate of initial arrangement. The second critical factor to consider is that competition may not result in mortality, but rather that plants of similar ages differ greatly in size (Mack and Harper 1977, Mithen et al. 1984). If this occurs, then plant size plant size should be positively correlated with distance between individuals (Antonovics and Levin 1980). Similarly, the spatial pattern of large, successful stems could be compared to the pattern obtained when large stems are assigned randomly from the set of all potentially successful individuals. Such a set would include both large and small stems of the same age. In this manner, instead of testing for random mortality, a hypothesis of random "success" is tested.

Fire is the primary natural disturbance in the boreal forest (Rowe 1961, Rowe and Scotter 1973, Bergeron and Dubuc 1989). Its action erases much of the standing vegetation, and initiates a rush to occupy space (Heinselman 1981). Such regeneration goes through a sequence of establishment and growth, each with its own spatial component (Houle 1995). Because propagules, like seeds from cones, and ramets of clones, are usually clustered in space, intraspecific competition is expected to be intense in the initial stages of forest recovery, as documented in aspen (Perala 1973, Pollard 1971), pine (Kenkel 1988, Kenkel et al. 1989), and spruce (Newton and Smith 1991, Newton and Joliffe 1998). For similar

reasons, interspecific competition is thought to be weak at this stage (Grubb 1977, Horn 1981, Rowe 1983), but may intensify as species begin interacting.

The presence of intraspecific and interspecific competition can be tested by examining the spatial arrangement of a species and the spatial relation between species, using a null hypothesis of random success. For example, intraspecific competition would be deemed to operate if the largest individuals within a species were regularly spaced with respect to all stems of the same age. Similarly, interspecific competition would result in spatial segregation of species in a bivariate analysis. In this chapter, two post-fire boreal forest sites of different ages are examined to see if such patterns can be detected at different times following the disturbance. Because intraspecific competition is likely to have been operating for longer period, I hypothesized patterns indicating this type of competition should be conspicuous. This means that, under a hypothesis of random success, large, successful individuals should be regularly arranged.

Methods

The younger site was a 21 year old post-fire area in central Alberta, near the Pelican Hills (55°,30' N, 113°,50' W). The soil profile consisted of relatively thin humic horizon (≤10 cm) on a gravelly sandy-silt inorganic substrate. The canopy consisted *Populus tremuloides* and *Pinus banksiana*, between approximately 6 m and 10 m. *Picea mariana* was also present, but less than 1 m in height, and because these stems would have had a relatively smaller effect on the larger, fast growing *P. banksiana* and *P. tremuloides*, the species was not considered in this study. The site was situated beside, and accessible from, a cleared corridor for an

underground pipeline installed in the previous two years. Trees from the two canopy species were mapped and age was determined by tree ring counts, in 0.5 m x 0.5 m quadrats of a 30 m x 40 m area. After mapping stems to a quadrat, they were either cut or cored as close to the ground as possible for determining age in the laboratory. To determine the age of a stem, the cross section was sanded with 60 then 120 grit sand paper on a belt sander. Hand sanding was done with 150-220 grit sand paper, and ring counts were made under a dissecting microscope to assign year of establishment. Stems were arbitrarily classified into two sizes, large (≥5 cm diameter at ground height [dgh]) and small (<5 cm dgh). The 5 cm size threshold was set based on my experience in determining the age of stems. Many large stems were twice this diameter.

A second site that was 39 year older was examined, to assess whether patterns occurred at different times following a disturbance. The data from this site came from a published account (Brodie 1993) of a 70 m x 70 m area in the subarctic Québec forest tundra zone. The three canopy species present, *Populus balsamifera*, *Picea mariana* and *Picea glauca*, were mapped in 1 m x 1 m quadrats, larger than those in the Alberta site, and age was determined by ring counts. Because this site was more than twice the age of the Alberta site, the division between large and small stems was at 10 cm diameter at breast height (dbh), rather than 5 cm dgh.

Data Analyses

Stems from each site were classified based on species, age and size. However, not all stems were considered. For each species, only stems that were equal to or older than the youngest

"large" stem were used, because this set represented the initial set of stems from which the "large" stems emerged. For example, the age of the youngest "large" *P. tremuloides* at the Alberta site, was 14 years. The spatial pattern of all these *P. tremuloides*, both large and small, made up the initial arrangement of stems before competition caused size discrepancies. Random success was then tested by examining the spatial arrangement of "large" stems in this arrangement.

In all spatial analyses, both univariate and bivariate, the same statistic was used, and calculated in the following manner. First, for all the stems of a particular class (e.g. large *P. tremuloides*, or small *P. banksiana*) the number of stems within a given radius *d*, of each individual was counted. In the univariate case, these stems were in the same class, in the bivariate case they were in a different one. These observed counts were compared to the median number expected in 500 realizations of a random model, and expressed as a standardized deviate i.e. (observed count - expected count)/ *s*, where *s* is the standard deviation of the 500 randomly generated values. The meaning of this spatial autocorrelation statistic is that the deviation of the observed value is measured in terms of standard deviations from the median, instead of the actually number of counts. This reduces confusion between analyses that generate random distributions with different variances.

Statistical significance, in the form of a *P*-value, was determined by the percentile that the observed value occupied on either side of the median (equivalent to a one-sided test). The reason for choosing the median as the measure of expectation was that an equivalent number of percentiles occurred on either side of it.

A statistically significant positive value in the univariate case, indicated that within

d units of a particular class of stems, more stems of the same class were found than were expected. A significant negative value indicated that fewer stems of the same class were observed than expected. In the bivariate case, a statistically positive/negative value indicated that within *d* units of stems in a particular class, more/less stems of another class were observed than expected. The results were displayed in a correlogram which showed the autocorelation statistic as a function of distance.

Random models were constructed based on two null hypotheses. The first was a hypothesis of complete spatial randomness (CSR) whereby stems occur randomly across the site with equal probability. The second null hypothesis was a model of random stem success. Random success models randomly assigned large stem status to all potentially large stems by randomly rearranging the size class label of each stem (i.e. "large" or "small"), while at the same time keeping the actual position of each stem fixed.

Lastly, as an alternative approach to examining the spatial pattern of species, particularly those associations in the immediate neighbourhood of large stems, a Least Diagonal Neighbour Triangulation (LDNT; Fraser and van den Driessche 1972, Dale 1999) was performed on the data from both sites. This procedure is computationally simple, and provides an objective means of defining the neighbours of each stem. However, it is usually applied to point patterns, and because stem positions reported here were in quadrats, I changed the data slightly by assigning each stem to a random position in its quadrat. This is one possible way of representing data in point pattern form after losing information by using the quadrat sampling method.

Once the triangulation procedure was complete (Figures 5-1, 5-2) and all neighbours

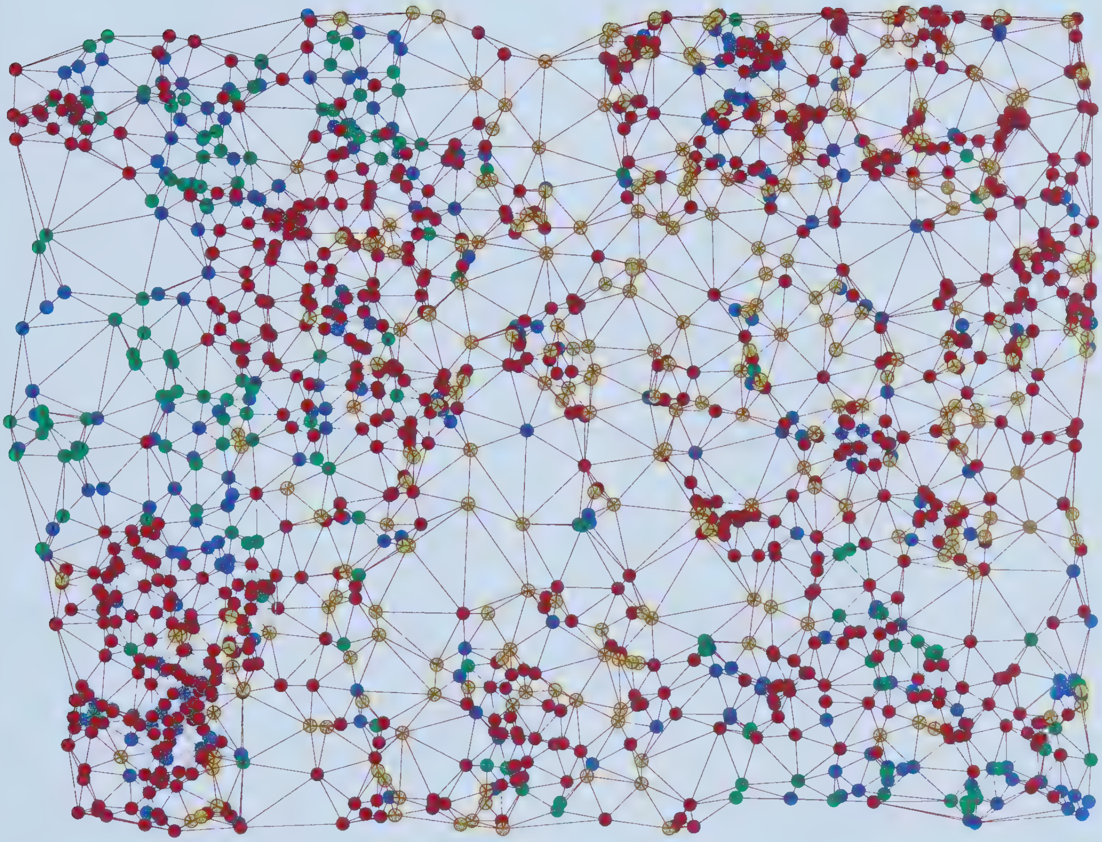

Figure 5-1. Stem positions of large and small *P. banksiana* and *P. tremuloides* in the Alberta site that were used to define neighbourhood relationships by Least Diagonal Neighbour Triangulation.

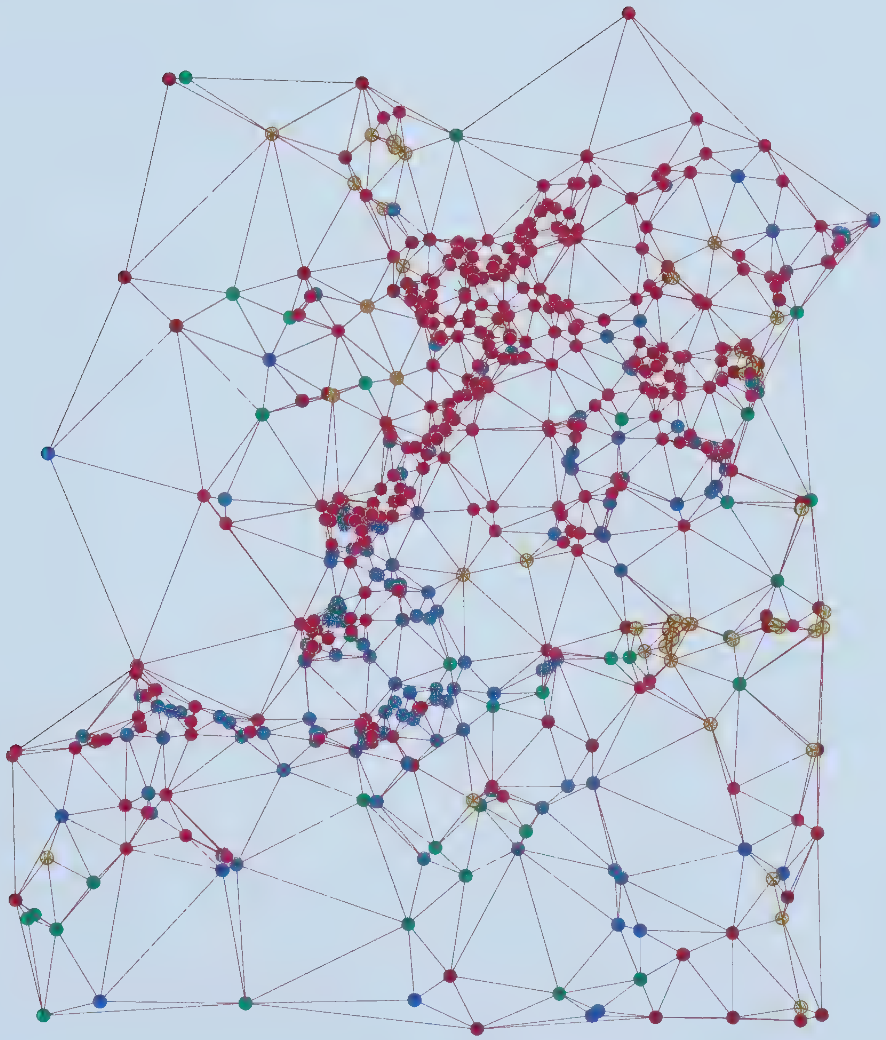

Figure 5-2. Stem positions of large and small *P. balsamifera*, *P. mariana* and *P. glauca* in the Alberta site that were used to define neighbourhood relationships by Least Diagonal Neighbour Triangulation.

were assigned, I examined the neighbours of each class of stems. In particular, the mean number of neighbouring stems per class, and the mean distance to them were calculated. These values were compared to the means obtained from 500 random rearrangements of the stems. Hypothesis tests again were one-sided, $\alpha=0.05$.

Results

Spatial Pattern under Complete Spatial Randomness

In the Alberta site, aspen showed a distinct J-shaped age class distribution, and pine a skewed unimodal distribution (Figure 5-3). Large aspen stems were generally older than large pine. Most of the pine were between 18 and 20 years with relatively few 21 year old stems compared to the aspen. The youngest large aspen stem was 14 years, and the youngest large pine, 11 years. All of the respective species stems these ages or older were considered to have the potential of gaining large status. However, most of them were small (i.e. <5 cm dgh), (Figure 5-3).

The spatial arrangement of each species is shown in Figure 5-4, and the spatial pattern analyses of large individuals from each species is shown in Figure 5-5. In both species, the large individuals were clustered, but at different scales. Patches, defined as the distance at which the most negative value occurs, were smaller for aspen at approximately 40 quadrats compared to the pine, which were about 55 quadrats. An aggregation of stems

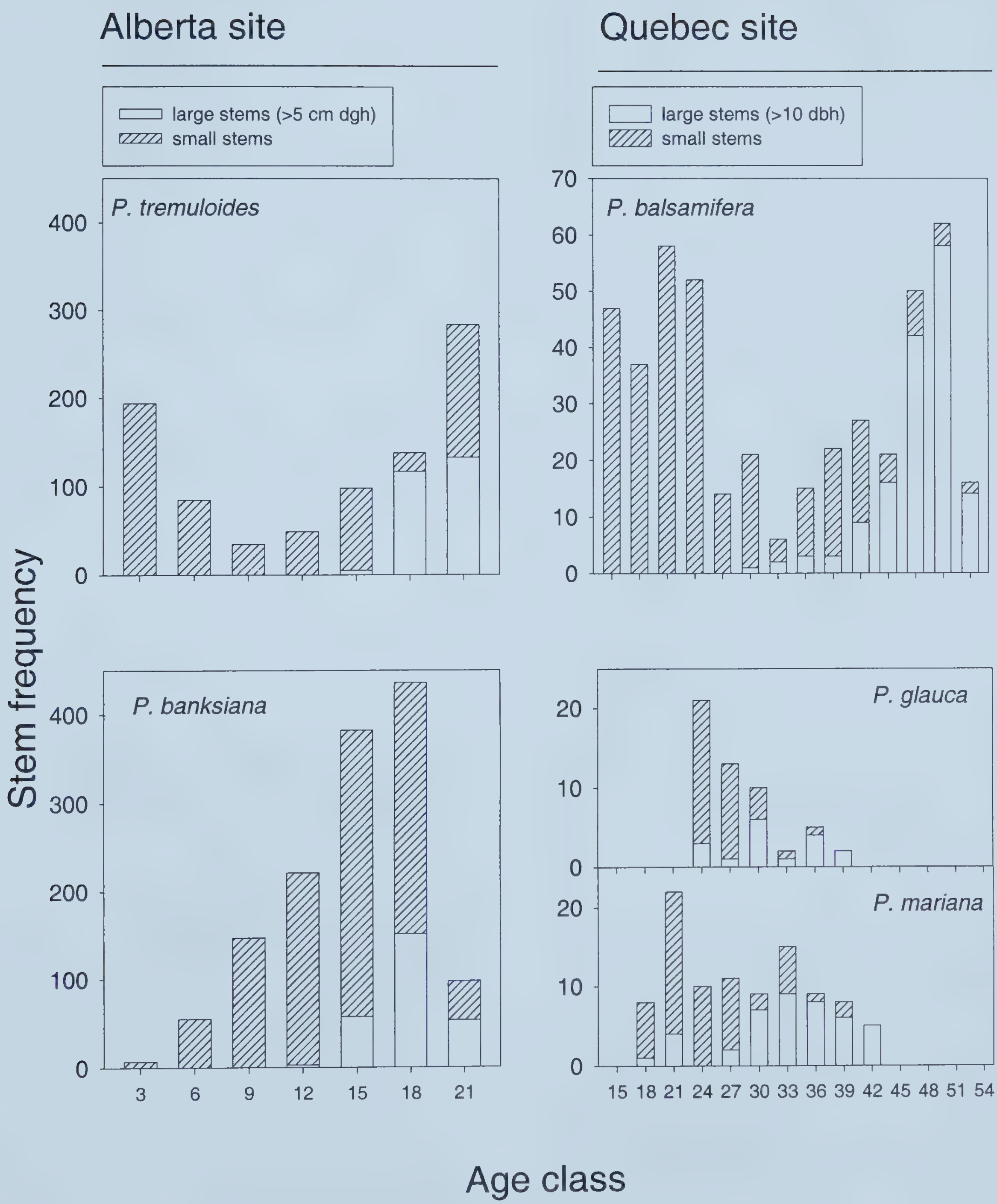

Figure 5-3. Frequency distributions of canopy trees species in 3 year old age classes, and 2 size classes, at the Quebec and Alberta sites.

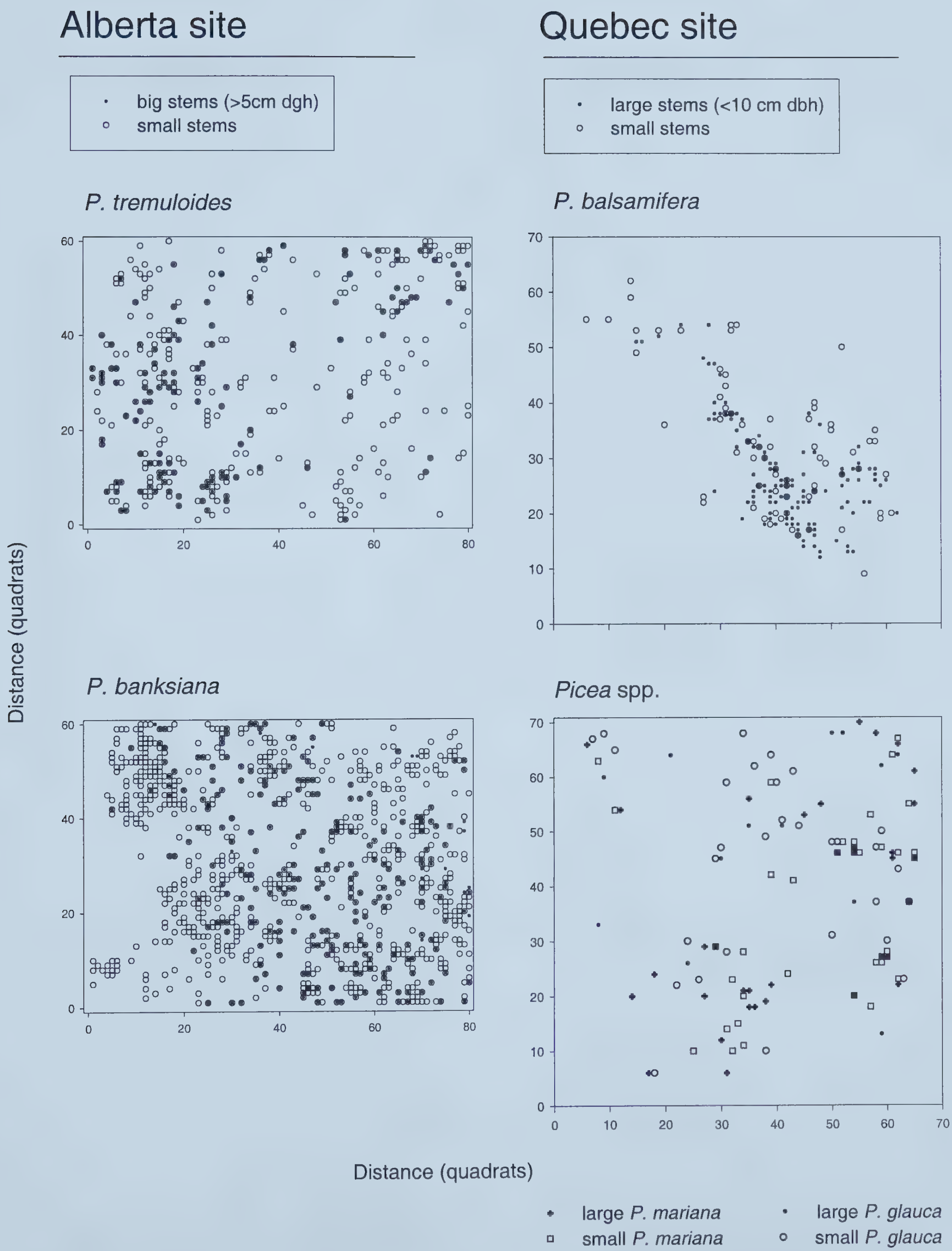

Figure 5-4. Spatial arrangements of the canopy species stems with the potential to obtain large status. Stem size class is indicated.

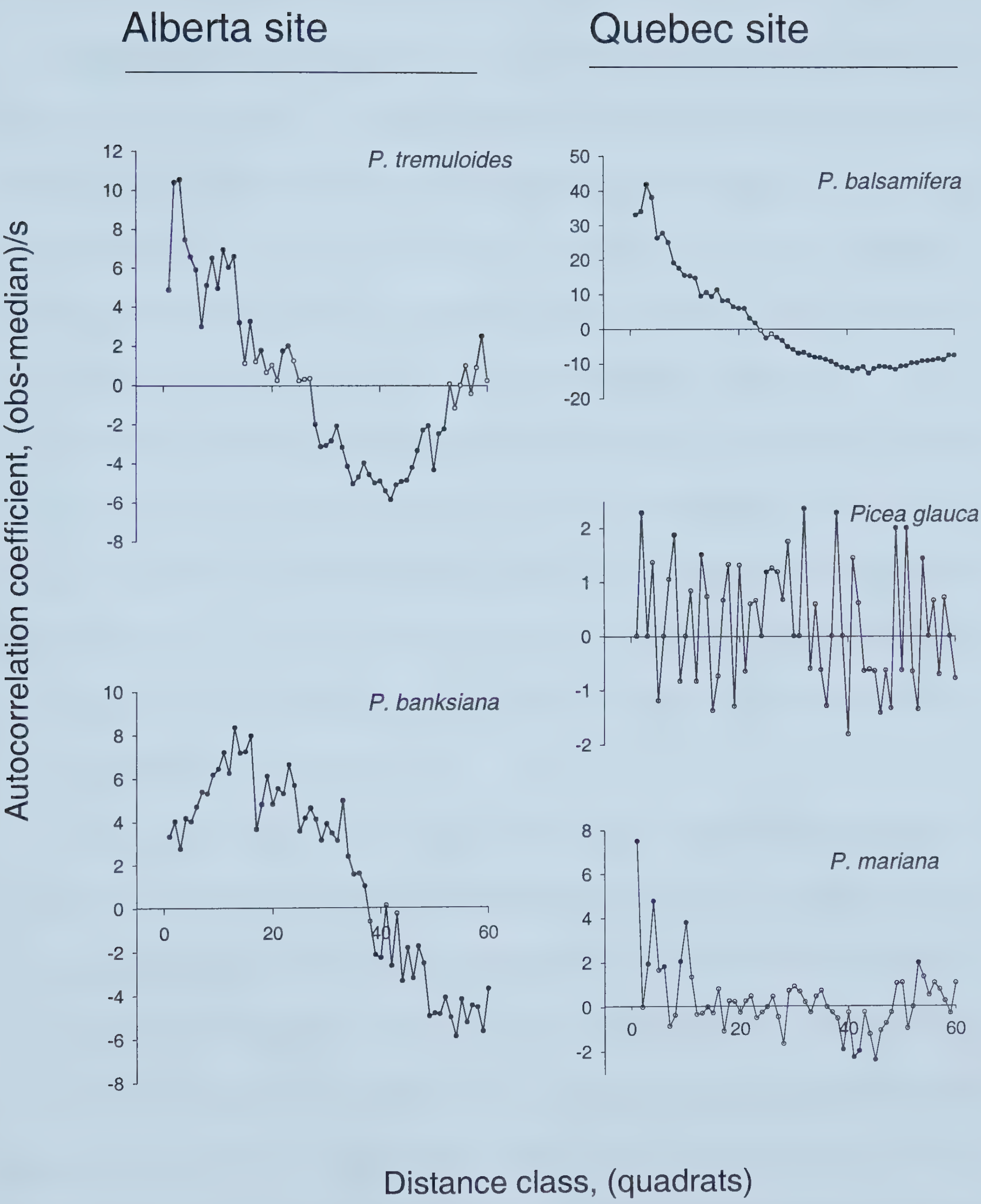

Figure 5-5. Univariate spatial pattern analysis, under a hypothesis of complete spatial randomness, for large individuals of the canopy species at both sites. Solid circles indicate statistically significant deviations from expectation (P <0.05, one-sided test).

at large distances indicated that there were several patches of large aspen stems, Figure 5-4.

Spatial association between the two species showed that large stems were highly segregated at close distances, and aggregated farther at about 50 quadrats (Figure 5-6), indicating an alternating pattern of species at the site (Figure 5-4). In particular, proceeding from the bottom left portion of Figure 5-4 to the top right, there is an area of large aspen, then large pine, then large aspen again. When large and small stems were combined, the spatial association between the two species is not much different (Figure 5-6).

The spatial distribution of *P. balsamifera* and the *Picea* spp., in the Québec site show the former as quite visibly clustered, and the two spruce species much less so (Figure 5-4). The age class distribution of the three species (Figure 5-3) are superficially similar to the Alberta site in that the deciduous *P. balsamifera* is bimodal, and the evergreen spruce tended to be unimodal. A major difference from the Alberta site, however, is the greater ratio of large to small stems in the older age classes.

Spatial pattern analysis of the large stems (Figure 5-5) confirmed that the *P. balsamifera* was clustered at a scale of about 40 quadrats. The spatial arrangement of the large spruce stems showed that *P. mariana* was clustered, and *P. glauca* showed no pattern.

In general, the large *Picea* species were each aggregated with *P. balsamifera* at a scale of about 60 quadrats (Figure 5-7). However, *P. glauca* and *P. balsamifera* were segregated from each other at closer distances. There was no relation between large stems of the two spruce species, however. When spatial association is examined irrespective of size class, the patterns were similar to the large stems.

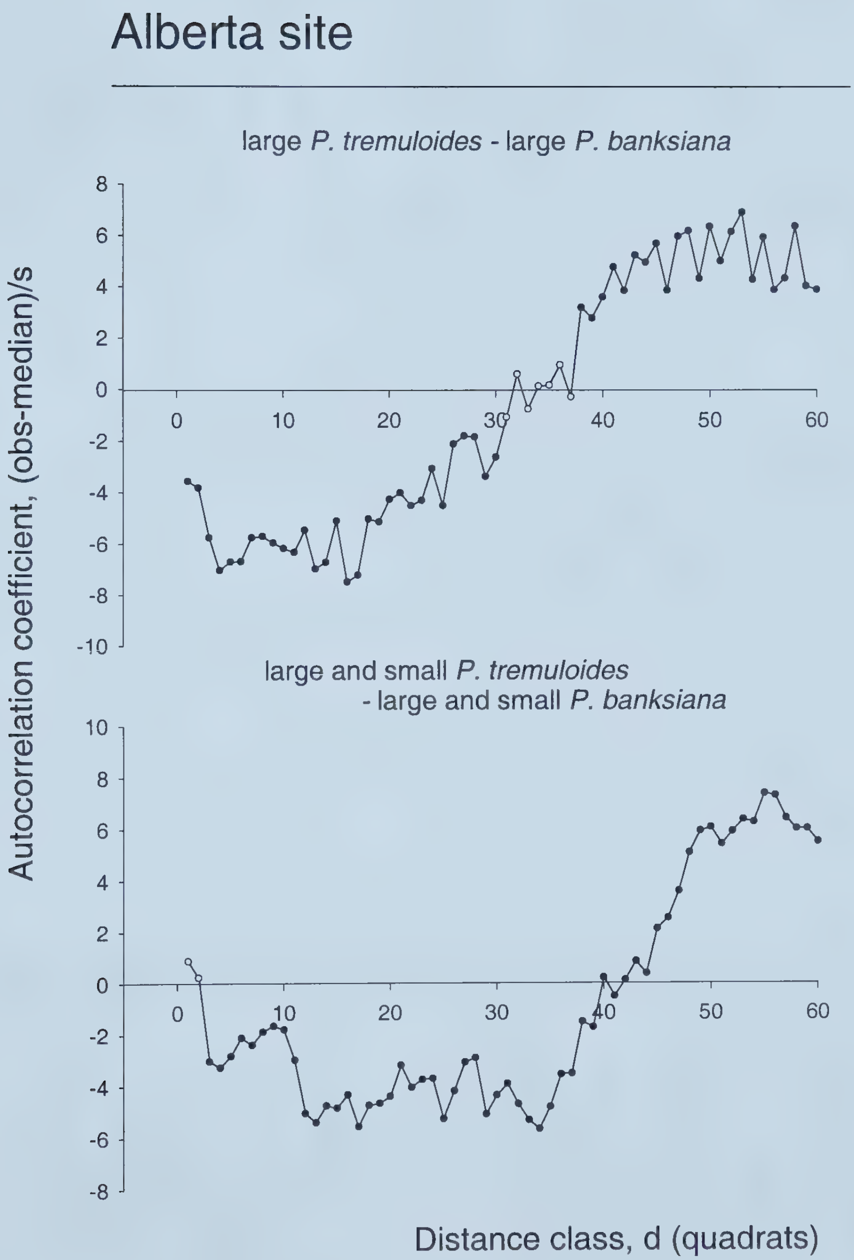

Figure 5-6. Bivariate spatial association under a hypothesis of complete spatial randomness between large stems of both species at the Alberta site, and between all stems of both species. Solid circles indicate statistically significant deviations from expectation (P <0.05, one-sided test).

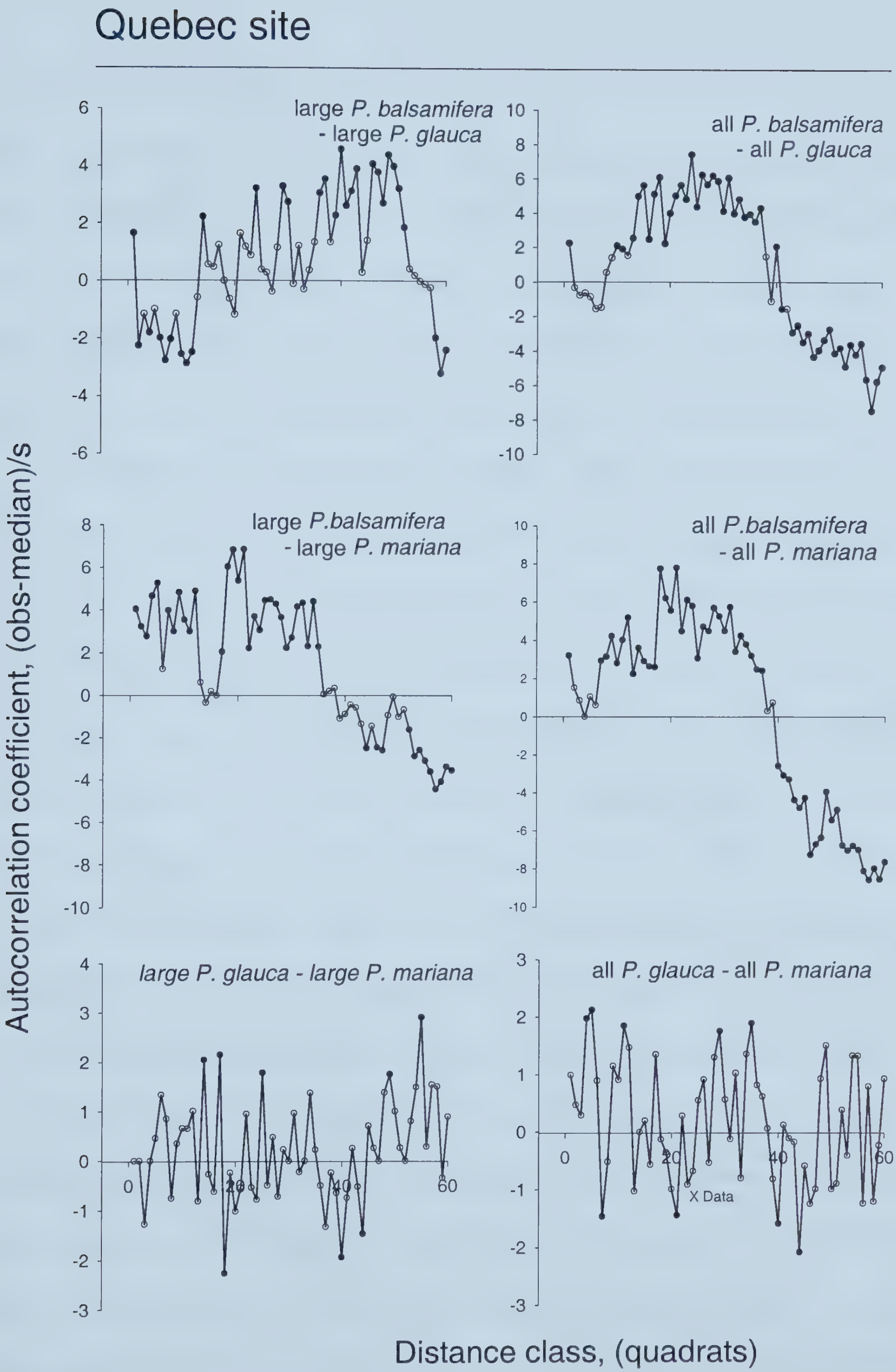

Figure 5-7. Bivariate spatial association under a hypothesis of complete spatial randomness, between large stems of each species pair, and all stems of each species pair, at the Quebec site. Solid circles indicate statistically significant deviations from expectation (*P* <0.05, one-sided test).

Spatial Pattern under Random Success

Under a null hypothesis of random stem success, big stems of both aspen and pine at the Alberta site tended to be either clustered or random at relatively close distances e.g. 1 to 10 (Figure 5-8). Combine the species, however, and large stems were over-dispersed at relatively small scales (Figure 5-8). The bivariate analysis between the two species show arge pine and aspen stems were segregated to a distance of about 40 quadrats (Figure 5-9).

In the Québec site, *P. balsamifera* were highly clustered to about the same distance as the CSR test (40 quadrats), but this time both *Picea* species appeared random. Analysis of large stems irrespective of species shows large stems that are highly clustered, reflecting a larger influence on the analysis of the more abundant *P. balsamifera* (Figure 5-8).

Bivariate analysis between *P. balsamifera* and the two spruce species tended to be strongly segregated (Figure 5-9), with the exception of a small interval at low spatial scale between *P. balsamifera* and *P. mariana*. The *P. balsamifera* and *P. glauca* were segregated to scale of about 50 quadrats, whereas *P. balsamifera* and *P. mariana* were segregated to a slightly greater scale. The spatial association between the two spruce species, similar to their association under CSR, did not differ greatly from random success at any scale (Figure 5-9).

Results from the LDNT approach are shown in Tables 5-1 to 5-4. For each class of stems these tables show the mean number of neighbours, or the mean distance to neighbours, of the other stem classes. Neighbours were defined by the triangulation method. The tables are not symmetrical because the number of stems in each class are not equal. For example, if one stem of class *A* were surrounded by four stems of another class *B*, then from the

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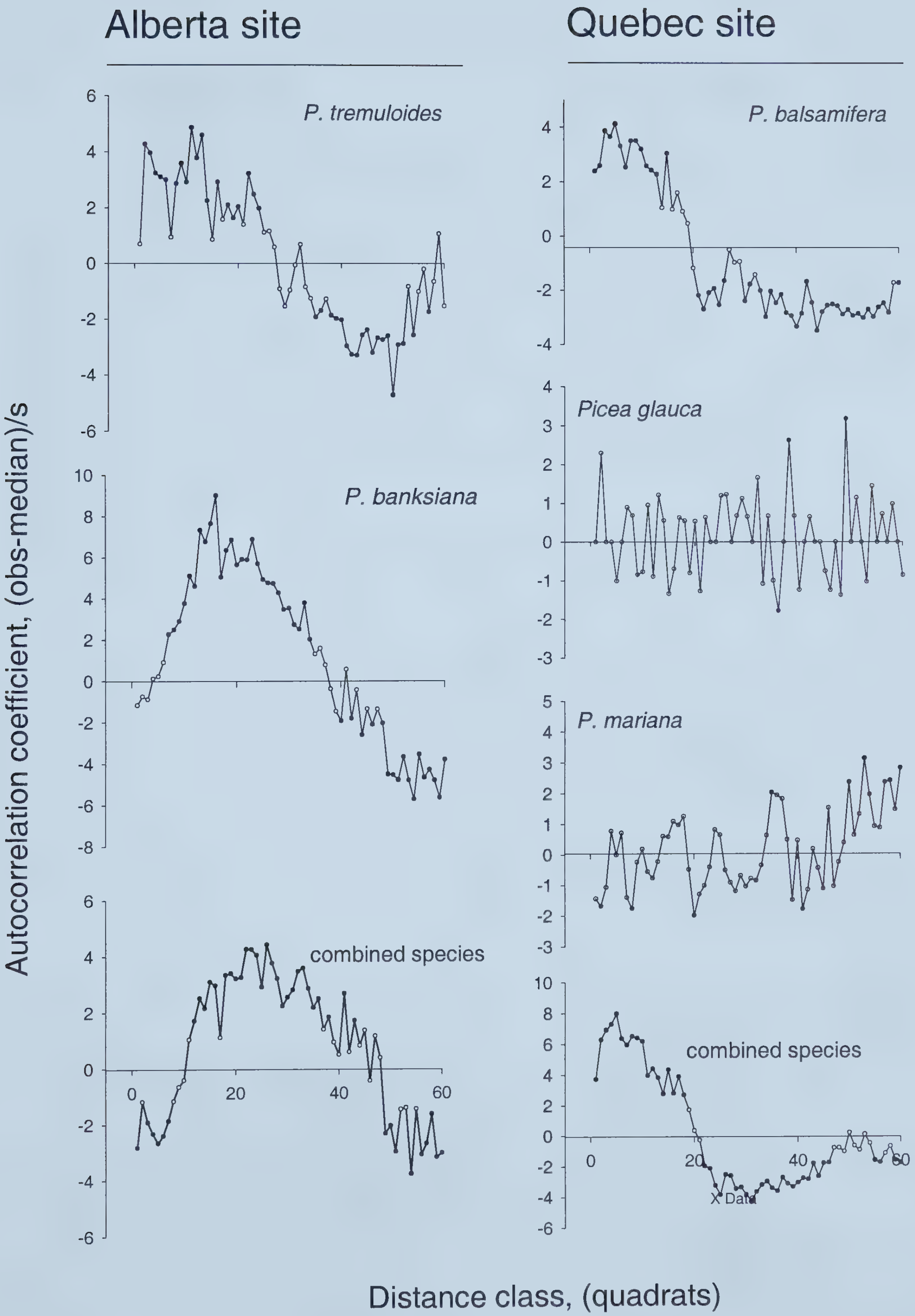
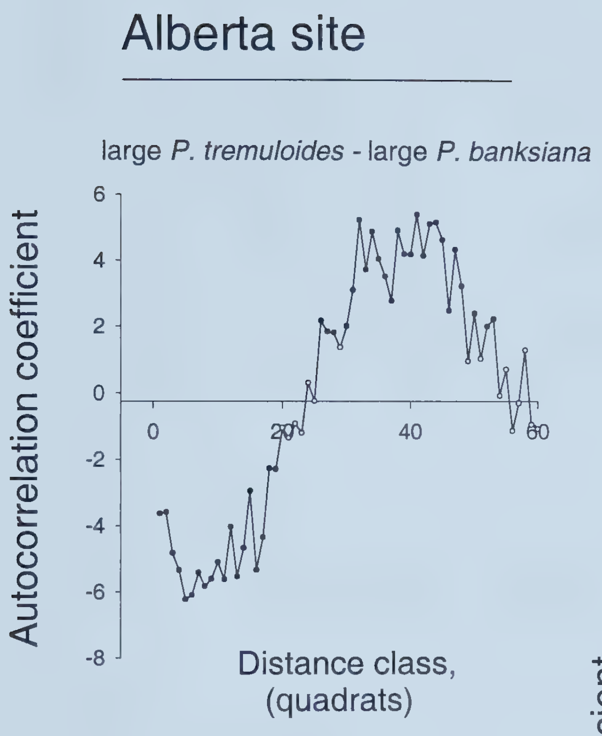


Figure 5-8. Univariate spatial analyses of canopy species at both sites under a null hypothesis of random success. Solid circles indicate statistically significant deviation from expectation (*P* <0.05, one-sided test).



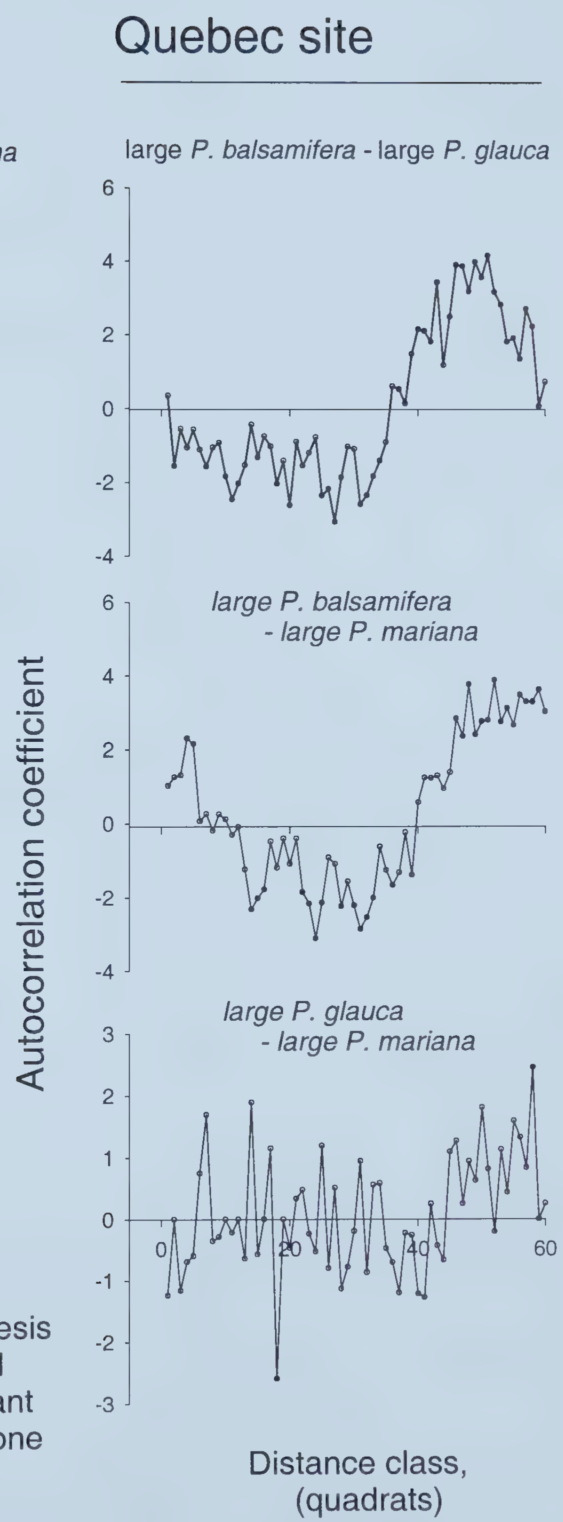


Figure 5-7. Bivariate spatial analyses between the large stems of different species combinations under a hypothesis of random success in both sites. Solid circles indicates a statistically significant deviation from expectation ($P < 0.05$, one -sided test).

Table 5-1. Mean number of neighbouring stems by stem class, that surround each stem of the focal stem class, in the Quebec data set. Neighbour relationship was derived according to a Least Diagonal Neighbour Triangulation. (o indicates that the observed mean number of neighbours did not significantly differ from expected under randomization of species and size labels. +, ++ and +++ indicate that the observed mean was significantly greater than expected with $P < 0.05$, $P < 0.01$ and $P < 0.005$, respectively.)

Neighbouring stem class:		*P. glauca*				*P. mariana*				*P. balsamifera*			
		small		large		small		large		small		large	
Focal stem class		mean		mean		mean		mean		mean		mean	
P. glauca													
	small	0.47	o	1.12	o	0.94	o	0.29	o	1.18	+	2.53	o
	large	0.53	o	1.33	o	1.08	o	0.72	o	1.28	++	1.14	o
P. mariana													
	small	0.38	o	0.93	o	1.14	o	1.60	o	0.48	o	1.38	o
	large	0.09	+++	0.47	o	1.22	o	2.04	o	0.38	o	1.40	o
P. balsamifera													
	small	0.14	o	0.32	o	0.14	o	0.16	o	2.31	+++	2.71	o
	large	0.08	o	0.13	o	0.19	o	0.25	o	1.26	+++	4.1	+++

Table 5-2. Mean distance from stems of the focal stem class to neighbouring stems by stem class, in the Quebec data set. Neighbour relationship was derived according to a Least Diagonal Neighbour Triangulation. (o indicates that the observed mean number of neighbours did not significantly differ from expected under randomization of species and size labels. -, -- and --- indicate that the observed mean was significantly less than expected with $P < 0.05$, $P < 0.01$ and $P < 0.005$, respectively.)

Neighbouring stem class:		*P. glauca*				*P. mariana*				*P. balsamifera*			
		small		large		small		large		small		large	
Focal stem class		mean		mean		mean		mean		mean		mean	
P. glauca													
	small	2.19	o	5.68	o	5.79	o	1.28	o	4.36	o	7.52	o
	large	2.68	o	7.87	o	5.45	o	3.11	o	4.91	o	4.92	o
P. mariana													
	small	2.34	o	4.67	o	6.03	o	5.06	--	1.85	o	3.68	o
	large	0.40	o	2.03	o	3.86	--	3.39	o	1.34	o	4.13	o
P. balsamifera													
	small	0.52	o	1.25	o	0.55	o	0.52	o	4.49	o	4.88	o
	large	0.42	o	0.58	o	0.50	o	0.74	o	2.27	o	7.56	o

Table 5-3. Mean number of neighbouring stems by stem class, that surround each stem of the focal stem class, in the Alberta data set. Neighbour relationship was derived according to a Least Diagonal Neighbour Triangulation. (o indicates that the observed mean number of neighbours did not significantly differ from expected under randomization of species and size labels. +/-, ++/-- and +++/--- indicate that the observed mean was significantly greate/lesser than expected with $P < 0.05$, $P < 0.01$ and $P < 0.005$, respectively.)

Neighbouring stem class:		*P. tremuloides*				*P. banksiana*			
		small		large		small		large	
Focal stem class		mean		mean		mean		mean	
P. tremuloides									
	small	1.54	o	1.07	o	2.55	o	0.76	o
	large	2.01	o	1.57	o	1.91	--	0.45	o
P. banksiana									
	small	0.80	o	0.32	o	3.71	+++	1.04	+++
	large	0.75	o	0.23	o	3.23	+++	1.85	o

Table 5-4. Mean distance from stems of the focal stem class to neighbouring stems by stem class, in the Alberta data set. Neighbour relationship was derived according to a Least Diagonal Neighbour Triangulation. (o indicates that the observed mean number of neighbours did not significantly differ from expected under randomization of species and size labels. +, ++ and +++ indicate that the observed mean was significantly greater than expected with $P < 0.05$, $P < 0.01$ and $P < 0.005$, respectively.)

Neighbouring stem class:		*P. tremuloides*				*P. banksiana*			
	Size	small		large		small		large	
Focal stem class		mean		mean		mean		mean	
P. tremuloides									
	small	2.80	+++	2.17	o	4.53	o	1.75	o
	large	4.06	+++	3.14	o	4.26	o	1.17	o
P. banksiana									
	small	1.43	o	0.72	o	5.89	o	2.14	o
	large	1.73	o	0.62	o	6.69	o	4.71	o

perspective of class *A* the mean number of *B* neighbours is 4, but from the perspective of class *B*, the mean number of *A* neighbours each *B* stem has is 1. To differentiate between the two perspectives, in the former case, class *A* is considered the focal class and *B* the neighbouring class, while in the latter case, class *B* is the focal class, and class *A* the neighbouring class.

The results from the LDNT method confirm much of the previous observations, but also give some new information. First, in the Québec site, large *P. balsamifera* stems tended to have more *P. balsamifera* neighbours both of large and small sizes than expected (Table 5-1). On the other hand, small ramets tended to have only more of other small ramets as neighbours. Therefore, although small ramets were clustered about large, large were not clustered about small. Small *P. balsamifera* also tended to surround *P. glauca* (Table 5-1). When neighbours are examined by distance instead of frequency (Table 5-2) the results show that neighbouring large and small *P. mariana* tended to be closer to each than expected, i.e. clustered.

In the Alberta site, pine generally had more of other pine as neighbours than expected, while large aspen appeared to have significantly fewer small pine as neighbours than expected (Table 5-3). Contrary to the relation between large and small *P. balsamifera* in the Québec site, the distance between large and small aspen in the Alberta site showed higher than expected distances (Table 5-4), indicating that small aspen tended to be segregated from all other aspen.

Discussion

The results of this study were somewhat surprising because the most successful stems of species were found generally clustered, not uniform as expected. At the same time, these stems were segregated from the most successful stems of the other species. Similar results have been shown by Peterson and Squiers (1995) for aspen (*P. tremuloides* and *Populus grandidentata*). In particular, they found that live aspen stems were clustered under a hypothesis of random mortality, and at the same time were segregated from white pine (*Pinus strobus*). Although they attributed this phenomenon to the clonal life form of aspen, the results presented here showed similar pattern for both clonal aspen and seed regenerating jack pine. Another explanation for these results is that the pattern expected from initial intraspecific thinning eventually became masked by interspecific relations such as competition or different tolerances in a heterogeneous environment.

Both intra- and interspecific competition probably occur to different degrees at different times following disturbance. Depending on the dgree and scale that species are segregated, in multi-species stands, intraspecific competition is most active immediately following disturbance, but decreases as initial clusters of ramets or seedlings from cones are thinned. As the survivors encounter others, some of different species, interspecific competition increases.

Increased interspecific competition would result in spatially segregated species. On the other hand, spatially segregated species may indicate either interspecific competition or different environmental requirements in a heterogeneous habitat. This latter case could be evidence of historic interspecific competition, which has resulted in resource partitioning

(Whittaker 1975, Antonovics and Levin 1980, Hartgerink and Bazzaz 1984, Dawson 1990). Any attempt of inferring process from pattern is tremendously difficult.

Monocultures have been described as going through two phases of competition: an initial "scramble" phase of symmetrical competition for space and resources leading to clumps of suppressed young individuals, followed by a "contest" phase of asymmetrical competition which results from size differences among individuals (Weiner and Thomas 1986, Kenkel 1988, Thomas and Weiner 1989). Two phase competition could also occur in species mixtures, such as those in this study, with the outcome dependent on whether interspecific competition currently occurs, or whether it occurred at some point in the past. Where interspecific competition currently operates, species composition in the contest phase would be uncertain and dependent on factors, such as initial floristics. Alternatively, where interspecific competition is not active but has resulted in resource partitioning, species composition would be dictated largely by environmental conditions and resource tolerance. In this case, there would be little interaction between habitats, and collectively species might be viewed as a single population going through two-phase competition.

In multi-species stands, the expected patterns that are absent in several single species examinations, are often found when species are combined and treated as one population (e.g. Watkinson 1986). This occurred in the Alberta site where a regular pattern of large stems of each species was expected, but clumped patterns were observed. Viewing all stems as a single population, however, showed regularly spaced large stems. Good and Whipple (1982) showed similar results, which indicate that some type of species interaction has occurred to influence their arrangement. For example, they may be better intraspecific competitors than

interspecific competitors.

Several aspects of this study differed from previous treatments of the subject. For example, data were gathered from a grid of quadrats, and although this made data collection systematic and relatively easy compared to true point mapping, the benefit was offset by the loss of spatial information at scales below the quadrat size. To compensate for this, a smaller size of quadrat was used at the Alberta site, which was younger and had smaller trees than the Québec site.

The method used to obtain the initial spatial arrangement of trees also differed from previous studies. For example, the combined arrangement of live and dead stems was not used for the initial arrangement, as in Kenkel (1988), because the Alberta site, of which I was primarily acquainted, had few dead stems; most were simply suppressed. Alternatively, the pattern of youngest stems was not used for the initial arrangement, as in Sterner et al. (1986), because it would require an assumption that establishment patterns do not change in time. In a forest developed from gap replacement, as in tropical rain forest, such an assumption might certainly be valid, but in post-fire boreal forest it would be questionable because initial establishment patterns are so vastly different from later establishment patterns. This is particularly true for post-fire *P. tremuloides* where an initial surge of sucker establishment occurs immediately after the disturbance, but substantially decreases with time (Brown and DeByle 1987) as soil temperature and light near ground level are reduced by shading (Peterson and Peterson 1992).

The approach to determine the initial arrangement of trees used the oldest age class of stems. The lower limit of this age class was defined by the youngest "large" stem. All

stems this age or older were thus believed to be initial establishers, and not disadvantaged because they established late. Despite this alternative approach, there were still at least two weaknesses to it. First, was the arbitrary size threshold assigned to define large stems. These thresholds had no biological basis. In the Alberta site, this value was based on experience from determining the age of stems, and in the Québec site it was arbitrarily doubled. Although I did not check, different results might be obtained by changing this value. Second, was the assumption that there was only size discrepancy and not mortality among stems. In reality, some small repressed stems probably died and so were not considered in the initial arrangement of individuals. Careful monitoring of all stems in an area through time could prevent this.

Two facts support that this second drawback operated to a greater degree in the Québec site than the Alberta site. First, most of the stems considered in the Québec site were in the large size class, but most in the Alberta site were small. Second, in the Alberta site, *P. tremuloides* displayed a J-shaped age class distribution rather than a reverse J-shaped distribution expected with more mature forests (Harper 1977). A J-shaped distribution indicated that, relative to the youngest age class, many of the older initial establishers were still present. Alternatively, Brodie et al. (1995) showed that *P. balsamifera* in the Québec site tended towards more of a reversed J-shaped age class distribution, indicating that many initial establishers had already died.

Forests are usually thought to be environments where competition, both intra- and interspecific, is greater above-ground than below-ground (Martens et al. 1997). Boreal forest soils are extremely variable and spatial association between soil factors and vegetation has

not been examined in great detail. Such an examination, however, could provide important additional information regarding the interspecific relations found in this study. For example, if the spatial segregation that was observed between species is due to habitat heterogeneity of the soils, and is an artifact of past interspecific competitive relations, then below ground relations between species may play a more significant role in boreal forest community composition than previously thought.

Whether competition in boreal forests is above- or below-ground, evidence of intraspecific competition was not found as expected, but may have been masked by the effects of interspecific relations as they became more prevalent. Determining when intraspecific competition ceases to dominate, and interspecific competition begins is an obstacle of examining multi-species areas (Connell 1983). Nevertheless, the results suggest a case similar to the Narcissus Effect (Colwell and Winkler 1984), a phenomenon originally shown in character displacement models of island biogeography. In this effect the role of competition is obscured by sampling from a post-competition "pool" because competition is already "reflected" in the pool. Thus, as Narcissus could not see to the bottom of the pool for his own image, and could not guess its depth, so the depth of intraspecific competition could not be determined for the image of post-intraspecific competition processes.

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CHAPTER SIX

Thesis Synthesis

Many types of pattern, at different levels of the biological hierarchy, are observable in space and time. In this work, I attempted to quantify and to characterize spatio-temporal pattern in boreal forest tree establishment, and then to make inferences about the processes that operate, such as clonal colonization. The initial approach was to use join count statistics. Joins were classified by two factors, one pertaining to a spatial interval and one to a time interval, but under certain circumstances the results were difficult to interpret. In the end, comparison of spatial patterns in different ages of trees allowed post-fire boreal forest establishment to be related to species regeneration strategy. This was followed by an examination of the degree to which competition operates on the initial post-fire establishers.

Although approaches using two-factor join count statistics have been used before (e.g. Gray et al. 1986), no statistical treatment of them had been done as Moran (1948, 1949) and Krishna-Iyer (1949, 1950) did for single factor joins. This was motivation for the work done in Chapter 2, which derived the mean and variance for a null hypothesis of random two-factor association among points on a lattice.

Subsequent use of join count statistics to measure rate of clonal expansion into a grassland proved successful. However, in more complicated circumstances it appeared that results were heavily influenced by young spatially clustered stems. Such biased results did not accurately reflect spatio-temporal associations among older stems. A second drawback

of using join count statistics was their inability to detect change in establishment. Therefore, they could not show where and when waves or surges of new stem establishment occur (e.g. Comtois and Payette 1987, Brodie et al. 1995).

Nevertheless, Klimes (1999) recently took a join count approach to examine small scale clonal growth in grasslands. His overall use of the method differed, however, because instead of using peaks in join classes to indicate rate of movement in a population, as was done in Chapter 3, he used the equivalence of an entire corellogram as the basis of classifying species growth forms. For example, clonal plants, like *Trifolium montanum*, showed positive significant peaks at almost all spatial and temporal intervals on the correlogram, whereas non-clonal species had far fewer. This means that clonal plants could establish in more places at different times than seed reproducing species, which had more restricted establishment.

One possible avenue of ecological analysis using join count statistics could be to use adjacency matrices and to define explicitly the neighbour relationship among cells. This was the approach to join count statistics recommended by Sokal and Oden (1978). The adjacency matrix for data on an m X n lattice has $(mn)^2$ cells, with each defining the importance, or weight, of a specific join between two cells on a lattice. In the join count method that I employed, an adjacency matrix was implicitly assumed, which consisted of equally likely, and equally weighted joins on the data lattice. Because there is often uneven distribution of stem establishment in time, an assumption of equally likely joins is probably not valid, and a modified adjacency matirix might be helpful.

Sokal and Oden (1978) discuss the explicit use of adjacency matrices in (one-factor)

join count statistics. The benefit of this approach is that an investigation of association on a lattice can be "designed". For example, the joins between certain cells, like the adjacent 1 and 2 year old stems in transect 3 of the Ministik Bird Sanctuary (Figure 3.1-2), might be weighted less than joins between older stems. Thus, an interval between two older stems would carry more weight in the resulting correlogram. The main drawback of using adjacency matrices is that they are computationally demanding, even by today's standards because the size of an adjacency matrix increases very rapidly as a lattice increases. For example, the adjacency matrix of a 3 X 3 lattice has an 3^4 elements, a 26 quadrat by 16 year lattice, like the one describing *P. balsamifera* expansion into grassland (Figure 3.1-2), would have a 173 056 element adjacency matrix, and the Alberta site, with a 80 X 60 quadrat spatial area over a 20 year period, would have an adjacency matrix with an order of 10^{10} elements. Each of these elements represents the degree, or weight, of association between a pair of cells on the data lattice. Even if such a matrix could be stored in computer memory, the human task of specifying the matrix "design" i.e. weights between each pair of cells on the lattice, would still be a large task, but perhaps it could be automated.

Two-factor join count statistics were not needed to conclude that post-fire boreal forest trees did not noticeably colonize from the disturbance edge. One of the main observations of this research supported Heinselman's (1981) statement emphasizing the importance of initial floristics in post-fire boreal forest establishment. For this reason the positions of a species' initial establishers were used as a basis for examining the spatial relations of different ages of conspecific stems. I hoped that this approach would indicate species "movement", and that these establishment patterns would correspond to dispersal and

survival strategy. The establishment of shade intolerant and clonal species showed greater response to their initial colonizers than shade tolerant and seed dispersed species. The overall results indicated that post-fire boreal forest population movement was more complex than I originally thought, and because in long term examinations of clonal expansion, surges in clonal establishment have been found instead of continual expansion (Comtois and Payette 1987, Brodie et al 1995), the idea of a constant rate of expansion is probably not valid as it was in the relatively short term expansion at Ministik.

Because establishment at different times of post-fire regeneration was examined from the spatial distribution of different ages of stems at a single point in time, there was a high probability that establishment of different ages of stems had been "filtered" through different amounts of competition. One reason for examining patterns of competition in the final chapter, therefore, was to assess the degree that patterns of initial establishers were influenced by competition.

Evidence for competition in initial establishers was taken from their spatial pattern. Competition in the patterns was measured against a null hypothesis derived from the Random Mortality Hypothesis (Sterner et al. 1986, Kenkel 1988, Peterson and Squiers 1995). A null hypothesis of random success was constructed because stem mortality was judged to have been largely incomplete. Instead, it appeared that size discrepancies were the major effect of competition. A test of random success compared the observed spatial relation among large, successful stems to the expected spatial relation among large stems when large size status was randomly assigned to the species. The results were unexpected, showing that large stems tended to be more clustered than over-dispersed, which would be expected if

intraspecific thinning operated. One explanation may involve interspecific relations because species tended to be segregated from each other. Such spatial segregation could be the result of response to habitat heterogeneity, or interspecific competition.

Pattern of individual plant establishment in space and time has an analogous counterpart at the population level. Metapopulations are collections of many spatially separated populations (Overton 1994), which, like the individuals within them, disperse, establish, and decline, spatio-temporally. Their dynamics are characterized largely by dispersal and establishment rates (e.g. Alvarez-Buyalla and Garcia-Barrios 1991) or mechanisms (e.g. Overton 1994), and in spatially explicit models, the rates of these depend on distance from a source population. Like results at the level of individuals, research on spatio-temporal pattern of populations has been active. For example, waves of population peaks have been claimed to travel through space for metapopulations of Scandinavian voles, and Canadian lynx (Ranta and Kaitala 1997, Ranta et al. 1997). Such work at both the individual and population levels may lead to better overall understanding of how processes operate at multiple levels. I believe that the results found in this research are new and important to ecology. This area of research appears currently active, and may provide fruitful methods of analysis, perspectives and knowledge of plant populations.

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